LAND USE AND PLANT SUCCESSION
IN COON VALLEY, WISCONSIN

JOHN B. MARKS

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INTRODUCTION

PURPOSE OF PROJECT

Men have been living in Coon Valley, Wisconsin, almost as far back in historical time as can be traced. They have lived under different systems of agriculture, different systems of land ownership, and different societies, but always they have lived from the land and within a framework of natural vegetation. The purpose of this study has been to determine just what effect these various peoples, societies, and land systems have had upon the direction and end of plant succession within the area.

SURVEY OF PAST WORK

The existing work on this subject is mostly scattered and inapplicable to this area. The great bulk of research on the relation of land use to plant succession has been done in the West. The work of A. W. Sampson (1919), Sarvis (1923), Forsling (1931), and Cooperrider and Hendricks (1937), traces the relations between good and bad land use and the natural vegetation.

The most notable work on the effect of grazing upon woods vegetation is that of Den Uyl, Diller, and Day (1938) and of Den Uyl and Day (1939). In general, the conclusion has been that woodland grazing is economically unjustified from the point of view both of trees and of livestock. For the effect of grazing upon Midwest prairies and meadows there is only the admirable paper of Homer Sampson (1921). Work on pasture vegetation has been more complete. The investigations of Skinner and Noll (1919), and Cooper (1932) have shown the effect of soil depletion and acidity upon the pasture flora. Parallel with this is the work of Warington (1924) in England. Recovery of eroded Ohio farmlands has been investigated by Larsen (1935).

Whoever investigates the vegetation of the Driftless Area must necessarily refer back to the work of Pammel (1905). Although much of his work does not apply specifically to Coon Valley, he must, nevertheless, be recognized as the first to grasp the general outlines of the floral groups within the Driftless Area.

The writer wishes to express his appreciation of the invaluable help and advice received throughout the development of this project from Professor N. C. Fassett of the Botany Department, University of Wisconsin, and from Professors O. S. Aamodt and H. L. Ahlgren of the Agronomy Department. The actual work on the project was made possible by a grant from the Alumni Research Foundation, University of Wisconsin, and through the cooperation of the United States Soil Conservation Service in the Coon Valley Area.

Photographs are by Lowell Gee of the United States Soil Conservation Service.

DESCRIPTION OF AREA

GEOGRAPHY AND SOILS

The Coon Valley Watershed lies in Vernon, La-Crosse, and Monroe counties in the southwest portion of Wisconsin within the Driftless Area. Elevations within the watershed vary from 643 feet on the Mississippi River terrace at Stoddard to 1,335 feet at Newry on the area's dividing rim. In general the topography of the area is typical of the whole of this driftless area of Wisconsin, Minnesota, Illinois, and Iowa. The region is nearing topographic maturity though there are still comparatively large areas of gently rolling upland on the ridges.

The soil series of the area naturally divide into two groups, those of the valley and those of the ridges 300 to 500 feet high. Of the ridge soil types the Clinton and Dubuque series represent soils developed under forest conditions, the former upon a loess substrate and the latter upon limestone. The Tama series, which occupies only a small portion of the ridge tops was developed upon loess under prairie vegetation. At the ridge bottoms adjoining the valley floor the Bates and Boone series developed upon the Jordan sandstone and upon colluvial debris, the first under prairie, the latter under forest conditions. On the second terraces the Bertrand and Waukesha represent the forest and prairie soils, respectively, while in the bottoms the light-colored Ray series develop upon alluvial material and the mucks are built up under the rank vegetation of the marsh meadow. Between the ridge and valley soils are large areas of slope with incomplete soil profiles, mapped as "rough, broken land."

CLIMATE

The climate of the area is summarized in Table 1. It is obvious that there are in the area two differing subclimatic types here in close juxtaposition, the ridge climate and that of the valleys or, as they are locally termed, the coulees. On the ridges (represented by the Viroqua station) the temperature, particularly in the spring and summer, is higher, probably because the ridges enjoy a longer daily period of sunlight than do the coulees (represented by the Hillsboro station). Precipitation in the valleys is slightly less than on the ridges and the growing season is considerably shorter in the cool frost-pockets of the coulees; the average frost-free season at Viroqua is 152 days, while at Hillsboro it is only 127 days. It is apparent that the ridges possess a hotter, drier climate than that of the coulees.

The rainfall regime rather closely follows the pattern characterizing the Plains or Missouri type; its curve is very nearly symmetrical and has its maximum in May. Isothermal maps make it plain that in yearly temperatures the area is transitional between

TABLE 1. Climatological data from Viroqua, Hillsboro, and LaCrosse. Based on long time averages.

VIROQUA*

Month	Temperature			Precipitation
	Mean	Absolute maximum	Absolute minimum	Mean
	°F	°F	°F	Inches
December......	20.7	54	—27	1.39
January........	15.0	55	—33	1.15
February......	16.9	56	—31	1.05
Winter.....	17.5	56	—33	3.59
March..........	33.0	79	—18	1.86
April...........	45.6	87	10	3.09
May...........	56.8	92	23	4.78
Spring......	45.1	92	—18	9.73
June...........	65.9	100	30	4.35
July...........	71.0	103	42	4.27
August........	68.6	100	35	3.66
Summer....	68.5	103	30	12.28
September......	60.8	95	21	3.89
October........	49.1	86	10	2.70
November......	33.5	70	—10	1.68
Autumn....	47.8	95	—10	8.27
Year.......	44.6	103	—33	33.87

*Mean date of last killing frost, May 5. Mean date of first killing frost, October 4. Mean length of growing season, 152 days. Latest spring frost, June 1. Earliest autumn frost, September 10.

HILLSBORO*

Month	Temperature			Precipitation
	Mean	Absolute maximum	Absolute minimum	Mean
	°F	°F	°F	Inches
December......	19.6	57	—32	1.43
January........	13.8	53	—45	1.39
February......	15.2	62	—44	1.27
Winter.....	16.2	62	—45	4.09
March..........	29.4	80	—26	1.86
April...........	44.3	86	4	3.02
May...........	55.2	91	21	4.60
Spring......	43.0	91	—26	9.48
June...........	64.7	100	25	4.43
July...........	69.2	106	35	3.66
August........	66.7	102	28	3.38
Summer....	66.9	106	25	11.47
September......	59.5	96	16	3.56
October........	47.6	87	4	2.45
November......	32.7	71	—15	1.64
Autumn....	46.6	96	—15	7.65
Year.......	43.2	106	—45	32.69

*Mean date of last killing frost, May 19. Mean date of first killing frost, September 22. Mean length of growing season, 127 days. Latest spring frost recorded, June 12. Earliest autumn frost recorded, August 30.

LACROSSE

Month	Sunshine		Relative Humidity		
	Actual hours	Percentage of sunshine possible	8 A.M.	12 M.	8 P.M.
Winter					
December......	111	41	84	71	83
January........	145	49	84	70	77
February......	156	54	83	67	70
Spring					
March.........	208	56	80	59	65
April..........	230	57	75	53	61
May...........	273	60	76	49	54
Summer					
June...........	297	63	75	57	60
July..........	333	71	83	55	61
August........	267	66	87	55	62
Autumn					
September......	218	58	87	57	66
October.......	179	52	84	57	72
November......	121	54	83	65	73

the Great Lakes climate to the east and the Plains climate to the west. Insolation is very nearly the same as that of a large portion of the Midwest, varying from 41 percent in December to 71 percent in midsummer. In general, the most striking feature of the climate is the remarkable parallelism in the trends of precipitation, temperature, and sunshine. In the relatively short growing season these three factors of plant growth reach a fortuitous maximum.

The area is, by hazard of position, in a region of tension between three of the great North American vegetative formations, the Lake States forest to the north and northeast, the oak-hickory formation to the south and southeast, and the prairie to the west. It is this peculiar position which gives it its rich variety of vegetative and soil types.

HISTORY OF COON VALLEY VEGETATION
ABORIGINAL PERIOD

The first people known to have lived in Coon Valley are only vaguely referred to as the "Hopewell Culture." Long before the beginning of recorded history they lived here practicing their primitive agriculture and building their mounds. Some time, perhaps a thousand years ago, one group of the Sioux succeeded them and continued, on an even more primitive scale, the cultivation the Hopewell group had begun. About 1665 two more Siouxan tribes, the Sacs and the Foxes, filtered into this area to farm their small patches and to hunt in the woods (Pease, 1909). Probably they used fires in their hunting, but just as probably they did not much affect the area's vegetation. It is known that the bulk of these tribes had settled along the Wisconsin near Prairie du Chien and thus they could not be a great disturbing factor in the Coon Valley Area.

Around 1750, these Indians were forced out by the Winnebagoes, a hunting tribe which had quite a pro-

nounced effect upon the region's vegetation. It was their custom to drive the game by the use of ground and brush fires which, in all probability, very often ran wild. Since the land was communal, tribal property, there were no private rights violated and so no individual labored to check the spreading flames. Beltrami (1828) gives a vivid picture of one of these repeated fires which must have continued until substantial white settlement:

"The vigorous fertility of these countries imparts such strength to the vegetation of the grass and brushwood, with which they are overspread, that they obstruct the march of the Indians and in spite of every precaution produce a rustling which awakens the wild beasts in their coverts.

"The Indians, who are not easily stopped by difficulties, set fire once a year to the brushwood, so that the surface of all the vast region they traverse is successively consumed by the flames.

"It was perfectly dark and we were at the mouth of the upper river Yahowa [Iowa] . . . The venerable trees of these eternal forests were on fire, which had been communicated to the grass and brushwood and these had been borne by a violent northwest wind to the adjacent plains and valleys. The flames towering above the tops of the hills and mountains, where the wind ranged with much violence, gave them the appearance of volcanoes, at the moment of their most terrific eruption; and the fire winding in its descent through places covered with grass presented an exact resemblance of the undulating lava of Vesuvius or Aetna."

This repeated burning continued over the period of a century was bound to have an effect. Established forests turned soon into just what Beltrami describes, "grass and brushwood." The early explorers' accounts agree well with this interpretation. Since they traversed only that part of the area which borders on the Mississippi their picture is a marginal one, but one which may serve fairly well as an index to the state of the vegetation of the entire area at that time. It is interesting to note that, although the entire west bluff and most of the east is now wooded, explorers from Father Guignas (1727—he says "The Mississippi from the mouth of the Ouisconsin ascending goes northwest. This beautiful river extends between two chains of high, bare, and very sterile mountains . . .") on to Zebulon Pike (1811) describe the river bluffs as "hill or rather prairie knobs." Pike says:

"In the division of the Mississippi which we had passed from La Prairie des Chiens, the shores are more than three-quarters prairie on both sides, or more properly speaking, bald hills, which, instead of running parallel with the river form a continuous succession of high perpendicular cliffs and low valleys . . . These hills and valleys exhibit some of the most romantic and sublime views I ever saw: but this irregular scenery is sometimes interrupted by a wide extended plain which brings to mind the verdant lawn of civilized regions . . . The timber of this region is largely birch, elm, and cottonwood, all the cliffs being bordered by cedars."

All these descriptions emphasize the fact that in the past some limiting factor prevented tree growth in many places where it is today conspicuous. History, Beltrami's account, and the common opinion of old settlers supply the limiting factor—Indian fires. The scarring of old trees shows the effect these ground fires had on established vegetation in exposed places. Forest vegetation surviving from aboriginal times is invariably in protected spots and never occurs on the ridges where fires could easily sweep in.

The vegetation, then, which the surveyors found when they entered this region in 1846 and 1847 was one developed under a system of communal land ownership, very primitive agriculture, and an economy based mainly on hunting and constant hunting fires. The surveyors found about half the area in scrub. The remainder comprised the great Westby or Coon Prairie to the south, the little scrub-surrounded prairies of the ridges, some slope and bottom woods, and the marsh and prairie lands of the bottoms and terraces. What timber existed on the ridges was probably in open groves thickly undergrown with brush.

It seems fairly certain that burning did not bring about the spread of prairie vegetation on the ridges. Vegetational history here seems to corroborate Transeau's statement (1935):

"Fire as an ecological factor seems to boil down to this: that in forest climates it retards development and may lead to scrub but it does not result in prairie."

Areas similarly kept in an apparently permanent scrub subclimax through repeated burning have been described by Lutz (1934) on the Sand Plains of New Jersey.

SCRUB

The surveyors' descriptions and the observation of present-day scrub subclimaxes within the area are the only guides to the appearance of this community at the time of settlement. Where the surveyors mapped scrub, today there is crop, pasture, or woodland.

Judging from the woods which have developed on scrub sites the community was probably dominated by juvenile red oak *(Quercus rubra)* only here and there overshadowed by white oak *(Quercus alba)*. The surveyors mention hazelbrush *(Corylus americana)* and prickly ash *(Zanthoxylum americanum)*, and from modern successions we can surmise that aspen *(Populus tremuloides, P. grandidentata)* and paper birch *(Betula papyrifera)* were present as well. Herb cover probably included grasses more typical of nearby prairies and such aggressive forbs as goldenrod *(Solidago canadensis)* and horsemint *(Monarda fistulosa)*.

MAPLE-BASSWOOD COMMUNITY

On steep northeast slopes, in small protected coves, on rough broken land, and on the Boone series there are, in the area, occasional patches of a woods type which obviously antedates white settlement. Many of the sparsely branched, forest-grown trees are over 200 years old. The trees are of all ages. The first surveyors recorded this community in their descrip-

tions and the early settlers acknowledged its presence when they named "Timber Coulee."

This community is a faciation of the widespread maple-beech association. Sugar maple *(Acer saccharum)* and basswood *(Tilia americana)* are usually predominant, though in some places various species of elm *(Ulmus americana, U. Thomasi,* and *U. fulva)* assume eodominance. Bitternut hickory *(Carya cordiformis)* is also important but it can nowhere be classified as a dominant. Canopy occupancy in this community is usually 90 percent or even more.

FIG. 1. Climax forest (maple-basswood type). Note absence of shrub layer, sunflecks, presence of understory and ferns. This woodland has not been grazed for many years if at all.

The characteristic structural feature of this community is the understory of species tolerant enough to survive under the deep shade (see Table 8) of the dominants. Ironwood *(Ostrya virginiana)* is the most widespread but blue beech *(Carpinus caroliniana)* and smaller trees of the dominants make up much of the understory.

The shrub layer is only scantly developed. Bladdernut *(Staphylea trifolia)* is the most prominent species but alternate dogwood *(Cornus alternifolia),* waahoo *(Evonymus atropurpureus),* beaked hazel *(Corylus cornuta),* and gooseberry *(Ribes Cynosbati)* occasionally occur. Younger individuals of the dominants, white elm in particular, form the rest of the shrub layer.

Among the herbs, perhaps the most striking characteristic of this community is the richness and abundance of its vernal and early aestival aspects. In May the forest floor is entirely covered with liverleaf *(Hepatica acutiloba),* false rue anemone *(Isopyrum biternatum),* spring beauty *(Claytonia virginica),* and bloodroot *(Sanguinaria canadensis).* Vernal species characteristic only of this community include Dutchman's breeches *(Dicentra Cucullaria),* squirrel corn *(D. canadense),* toothwort *(Dentaria laciniata),* yellow adder's tongue *(Erythronium americanum),* bedstraw *(Galium Aparine),* and wild leek *(Allium tricoccum).*

As the growing season progresses, sweet cicely *(Osmorhiza Claytoni)* becomes by far the most important herb, but numbers of ferns thrive in deep

TABLE 2. Line transect counts of various species in the maple-basswood association.

Species	Communities							
	Aboriginal				Disturbed		Recovery	
	1	2	3	4	5	6	7	8
HERBS								
Acalypha virginica	....	....	....	....	4	....	....	....
Acer saccharum	1	6	10	1	3	2	2	2
Actea rubra	....	1	1	....	....	....	....	1
Adiantum pedatum	10	14	24	22	....	....	....	....
Allium tricoccum	2	....	....	....	....	....	....	....
Amphicarpa bracteata	....	....	1	....	....	4	1	10
Aralia nudicaulis	....	....	....	1	....	....	1	....
Aralia racemosa	....	....	....	1	....	....	....	....
Arisaema triphyllum	....	....	....	1	....	....	1	....
Asarum canadense var. acuminatum	5	1	5	11	....	....	....	....
Aster sp.	4	3	4	....	....	6	8	5
Athyrium acrostichoides	3	1	....	7	....	....	....	....
Athyrium angustum var. rubellum	3	3	....	....	....	....	....	5
Botrychium virginianum	....	....	....	....	....	....	....	3
Carex albursina*	8	3	10	8	....	4	2	23
Carex Hitchcockiana*	6	5	....	....	....	....	....	10
Carex laxiflora*	19	6	....	....	....	....	5	....
Carex mirabilis*	....	....	....	....	....	....	2	....
Carex pennsylvanica*	....	1	....	....	....	....	14	....
Carex rosea*	2	....	....	....	59	26	15	1
Carya cordiformis	6	6	2	....	....	....	2	8
Caulophyllum thalictroides	2	1	5	10	....	....	....	....
Circaea latifolia	....	....	....	10	25	38	52	20
Cornus alternifolia	....	....	1	1	....	....	....	....
Cryptotaenia canadensis	3	....	2	....	8	2	2	1
Cystopteris fragilis	14	31	3	2	1	1	....	....
Desmodium acuminatum	....	....	1	1	....	....	....	....
Erigeron ramosus	....	....	....	....	....	....	2	....
Eupatorium maculatum	....	....	....	....	....	....	4	....
Eupatorium rugosum	....	....	....	....	29	42	5	5
Evonymus atropurpureus	....	2	....	....	....	....	....	....
Fraxinus americana	....	....	....	....	....	....	8	1
Galium Aparine	....	....	....	2	....	....	....	....
Galium triflorum	3	....	....	2	3	1	2	9
Geranium maculatum	15	2	....	....	....	....	2	12
Geum canadense	....	....	....	2	2	1	....	8
Helianthus tracheliifolius	....	....	....	....	1	....	....	6
Hepatica acutiloba	13	31	10	5	....	1	....	25
Hydrophyllum appendiculatum	....	....	9	....	....	....	....	....
Hydrophyllum virginianum	8	5	4	12	....	....	....	2
Impatiens pallida	....	....	....	....	....	....	19	....
Laportea canadensis	....	....	....	10	....	....	....	....
Lappula virginiana	....	....	....	....	....	3	....	....
Melica mutica*	....	1	....	1	....	....	9	8
Mitella diphylla	14	26	16	6	....	1	....	2
Nepeta Cataria	....	....	....	....	1	....	....	....
Oryzopsis racemosa	2	1	....	....	....	....	....	....
Osmorhiza Claytonia	34	36	35	40	....	....	30	23
Osmunda Claytoniana	....	1	....	....	....	....	....	....
Ostrya virginiana	5	8	....	....	....	....	8	6
Oxalis europaea	....	....	....	....	....	....	2	....
Panax quinquefolium	....	....	....	....	....	....	1	....
Parietaria pennsylvanica	....	....	....	....	2	....	....	....
Parthenocissus vitacea	4	1	10	6	....	....	....	....
Phlox divaricata	5	....	....	....	....	....	....	....
Pilea pumila	....	....	....	....	53	....	8	7
Podophyllum peltatum	1	2	1	1	....	....	....	....
Polygonatum pubescens	1	....	1	11	....	....	....	1
Polymnia canadensis	....	....	....	2	....	....	....	....
Prenanthes alba	....	....	....	....	....	....	....	1
Pteretis nodulosa	....	....	2	1	....	....	....	....
Quercus rubra	....	....	2	....	....	....	....	....

*Estimates of grasses and sedges are necessarily inaccurate under grazed and recovery conditions.

TABLE 2 (continued)

Species	Communities							
	Aboriginal				Disturbed		Recovery	
	1	2	3	4	5	6	7	8
HERBS (Cont.)								
Ranunculus septentrionalis..	3	1	...	...	...	...	...	...
Ribes Cynosbati............	1	2	1	...	...	...	...	1
Sanguinaria canadensis.....	...	...	...	1	...	...	23	7
Sanicula gregaria.........	7	...	11	...	2	2	11	4
Sanicula trifolia..........	1	1	...	4	...	...	...	...
Smilacina racemosa........	7	1	...	18	...	...	...	1
Smilax herbacea...........	...	1	...	...	...	...	...	...
Solidago latifolia..........	...	...	...	...	...	...	...	5
Staphylea trifolia..........	1	1	...	4	...	...	...	...
Taraxacum officinale.......	...	...	...	...	...	...	2	...
Thalictrum dioicum........	...	...	...	...	...	...	1	1
Tilia americana	...	...	...	...	3	2	21	2
Trillium grandiflorum......	4	14	4	5	...	...	...	2
Ulmus americana..........	1	4	6	...	3	8	1	1
Urtica gracilis............	...	...	...	...	1	1	...	...
Uvularia perfoliata	1	3	12	8	...	...	...	3
Viola cucullata...........	...	1	2	...	12	15	2	...
Viola eriocarpa...........	...	3	...	1	...	...	8	32
TREES								
Acer saccharum...........	3	1	6	8	6	6	5	1
Carya cordiformis.........	1	1	...	...	...	...	...	...
Fraxinus americana.......	...	...	...	...	...	...	...	1
Fraxinus nigra...........	...	...	...	...	1	...	...	...
Juglans cinerea...........	...	...	...	...	1	...	...	...
Ostrya virginiana.........	...	...	...	...	...	...	2	1
Tilia americana...........	1	2	3	2	...	1	...	3
Ulmus americana.........	1	2	...	...	2	1	...	...
UNDERSTORY								
Acer saccharum...........	...	...	...	3	...	...	...	3
Carpinus caroliniana.......	...	4	...	...	...	...	...	...
Carya cordiformis.........	...	...	1	1	...	...	...	...
Ostrya virginiana..........	2	2	4	3	...	...	...	4
Tilia americana...........	2	1	...	...	...	...	...	...
Ulmus americana..........	3	4	...	...	...	...	...	...
SHRUBS								
Acer saccharum...........	...	...	...	2	...	...	...	...
Carpinus caroliniana.......	...	3	...	...	...	...	...	...
Carya cordiformis.........	...	...	2	...	...	...	...	...
Cornus alternifolia	...	2	2	...	...	...	...	...
Corylus cornuta..........	...	...	...	2	...	...	...	...
Ostrya virginiana..........	2	...	...	1	...	...	...	...
Ribes Cynosbati...........	...	1	...	1	...	...	...	...
Staphylea trifolia..........	...	2	1	12	...	...	...	...
Tilia americana...........	...	1	...	...	...	...	...	...
Ulmus americana..........	6	4	2	1	...	...	...	...

Notes on Communities:
  1 and 2 – North-facing slope.
  3 and 4 – Northeast slope.
  5 and 6 – Grazed with canopy disturbed.
  7 and 8 – Under five-year contract to Soil Conservation Service.

shade on the light, fertile soil. Fragile fern (Cystopteris fragilis) and maidenhair (Adiantum pedatum) are the most widespread, though various species of Athyrium (A. angustum var. rubellum, A. angustifolium, and A. acrostichoides), Dryopteris (D. spinulosa and D. Goldiana) and ostrich fern (Pteretis nodulosa) are also important.

A number of species of sedge (Carex plantaginea, C. albursina, C. Careyana, C. Hitchcockiana, and C. laxiflora) in this area are confined to this woods type. Some other characteristic herbs are mitrewort (Mitella diphylla), wood nettle (Laportea canadensis), wild ginger (Asarum canadense var. acuminatum), waterleafs (Hydrophyllum virginianum, H.

appendiculatum), black snakeroot (Sanicula trifoliata), Solomon's seal (Polygonatum pubescens) and blue cohosh (Caulophyllum thalictroides).[1]

OTHER WOODS TYPES

Two other woods types, probably dating from this aboriginal period, yet persist within the area.

Bottom Woods.—The bottom woods, dominated by white elm, were noted by the original surveyors. On many sites this community undoubtedly antedates white settlement but its existence in places originally mapped as marshland indicates that it has spread since the first survey. Typically this community is confined to the higher bottoms on the Bertrand series. It has been universally pastured so that any picture of its original aspect must be largely conjecture.

FIG. 2. Red oak woods type—ungrazed. Note prominent shrub layer, sunflecks, and the lack of understory structure. The white oaks (approx. 200 years old) are open grown. The red oaks (60 to 80 years old) are forest grown.

In structure and species composition this woods type is very similar to the maple-basswood community. The dominant tree species here is largely Ulmus americana but there are many individuals of black maple (Acer saccharum var. nigrum) and bur oak (Quercus macrocarpa). Altered as most of these areas are, the understory or shrub layer cannot be described beyond saying that the Staphylea trifolia and Zanthoxylum americanum now present probably represent relicts from the original woods. Herb cover was probably very similar to that of the maple-basswood community, minus some of the most delicate species such as the Athyriums which might be injured by infrequent floodings. This elm-dominated type may be considered as a modification of the maple-basswood community under the peculiar conditions of the river bottoms.

White Pine Type.—The second of the two minor aboriginal woods types is probably the most closely confined of the entire area. It occurs only under very specialized conditions of soil and exposure. In the bottoms of the larger valleys the stream often cuts steep, overhanging cliffs in the Jordan sandstone.

[1] See Table 2 for line transects of this community. Unfortunately the transects had to be made in midsummer so that only the Hepatica shows of all the numerous vernal species.

When these face north and when the cool stream flows immediately at the base, these bluffs have a local climate quite different from that of any other areas within the region. Insolation is reduced to a minimum and the midsummer temperature may be as much as 10° F. cooler beneath the bluff than at its summit. The average summer temperature here probably is below the 70° F. postulated by Köppen as the summer isotherm limiting the southward extension of the northern forest. These peculiar conditions bring about a specialized vegetation type, which, judging from the age of the trees, was present long before settlement.

This community may be recognized from afar, for its dense stand of white pine *(Pinus Strobus)* contrasts boldly with the bluffs. Under the pines there is often an understory of paper and yellow birches *(Betula papyrifera* and *B. lutea)*, mountain maple *(Acer spicatum)*, basswood *(Tilia americana)*, and ironwood *(Ostrya virginiana)* as well as younger individuals of white pine. The well-developed shrub layer includes individuals of mountain maple, yew *(Taxus canadensis)*, bush honeysuckle *(Diervilla Lonicera)*, nannyberry *(Viburnum Lentago)*, and several other species. Some of the characteristic herbs are bulblet fern *(Cystopteris bulbifera)*, Canada mayflower *(Maianthemum canadense)*, cornel *(Cornus canadensis)*, northern bedstraw *(Galium boreale)*, rock brake *(Cryptogramma Stelleri)*, and goldenrods *(Solidago latifolia* and *S. sciaphila)*. Probably the most interesting characteristic of this list of species is the number which have their centers of range far north of the Coon Valley Area. It should be noted here, too, that it is on these bluffs that many of the Driftless Area endemics, such as *Solidago sciaphila*, *Aconitum novaboracense* var. *quasiciliatum*, and *Dodecatheon amethystinum*, are found.

UPLAND PRAIRIES

On the ridges, in the midst of scrub and scattered timber, the first settlers found occasional stretches of prairie, but it is fairly certain that these upland prairies occupied only a small portion of the ridge tops. Early testimony avers that these ridge tops were scrub and the soil type covering the greater part of their area, the Clinton, is a forest soil. If there were extensive prairies on the ridge tops in the Coon Valley Area—as is known to have occurred in the region south of Westby—then prairie species would persist as reliets in protected spots such as roadsides. Prairie reliets are frequent and well-distributed along roadsides in the old Westby prairie (see Table 3) but on the Coon Valley ridges the writer knows of only two places where big bluestem *(Andropogon furcatus)* persists.

Goat Prairies and Juniper Flats.—The most striking of the upland prairies are the so-called "goat prairies" usually located on dry, hot southwest slopes so steep that only the nimble goat could graze them. These areas are plainly marginal to the main body of the upland. Pammel (1905) and Shimek (1910) have described these prairies within the Driftless

TABLE 3. Number of prairie relicts observed along twenty miles of roadside on site of former Viroqua prairie.*

Amorpha canescens	1
Andropogon furcatus	16
Andropogon scoparius	5
Geum striatum	1
Helianthus giganteus	12
Potentilla arguta	9
Silphium laciniatum	2
Silphium perfoliatum	1
Silphium terebinthaceum	1
Sorghastrum nutans	9
Stipa spartea	4

*These represent colonies of individuals, not single plants. The author knows of only two places on the ridges above Coon Valley which have any colonies whatsoever to compare with these seen in the course of an hour's ride along country roads.

Area. Vestal (1918) and Hanson (1922) have studied similar areas outside it. At Coon Valley these prairies have, through their steepness, been protected from grazing, even though many of them actually are within the fence lines of wood pastures. Since they exist on such steep slopes, their soils necessarily have truncated profiles and often there are rock outcrops. The primary stages of the xerosere appear here but they are so small in area that they have little importance in land use.

The structure of these prairies is naturally less complex than that of the communities which have already been described. There is no tree or understory layer; the shrubs include only two species, red cedar *(Juniperus virginiana)* and creeping juniper *(J. communis* var. *depressa)*, and it cannot be said that these truly belong to this community. The herb layer is quite definitely dominated by grasses, *Andropogon furcatus*, little bluestem *(Andropogon scoparius)*, and Indian grass *(Sorghastrum nutans)* which here all grow in clumps, together with sideoats and hairy grama *(Bouteloua curtipendula* and *B. hirsuta)* which seem usually to adopt the sod habit. Among these grasses grow a number of characteristic forbs, *Potentilla arguta*, bush clover *(Lespedeza capitata)*, thimbleweeds *(Anemone virginiana* and *A. cylindrica)*, prairie clovers *(Petalostemum purpureum* and *P. candidum)*, lead plant *(Amorpha canescens)*, and *Coreopsis palmata*. The only indication of well-defined seasonal aspects is given by the early blooming Pasque flower *(Anemone patens* var. *Wolfgangiana)* and bird's foot violet *(Viola pedata* var. *lineariloba)*.

Around the limestone crags in the most exposed and most desiccated portions of these southwest slopes are the juniper flats. This is a specialized community dominated by the bushy *Juniperus virginiana* and probably differing from the goat prairie, with which it is usually closely associated, by a slight but significant difference in microclimates. There are few shrubs beside the juniper though an occasional *Diervilla Lonicera* may appear. In the rock crevices grow sedge *(Carex eburnea)*, *Zygadenus chloranthus*, bulblet fern *(Cystopteris bulbifera)*, bluebell *(Campanula rotundifolia)*, rock brake *(Pel-*

laea glabella), rock cress *(Arabis lyrata)*, columbine *(Aquilegia canadensis)*, goldenrod *(Solidago hispida)*, and pellitory *(Parietaria pennsylvanica)*.

Ridge Prairies.—The upland prairies on the level ridge tops can be described only from relicts. Apparently big bluestem was the dominant and formed a sod in many places. Little bluestem and Indian grass were present as well but were important only on dry knolls where they shared dominance with needlegrass *(Stipa spartea)* and probably with grama *(Bouteloua* spp.). Here, too, many forbs are found, some new, such as compass plants *(Silphium laciniatum, S. terebinthaceum)*, cupplant *(S. perfoliatum)*, giant sunflower *(Helianthus giganteus)*, yellow avens *(Geum strictum)*, and meadow parsnip *(Zizia cordata)*, along with many forbs already noted on the goat prairie.

VALLEY MARSH AND PRAIRIE MEADOWS

The last of the aboriginal communities are the valley marshes and prairies situated in the low coulee bottoms and about the edges of sloughs, mostly on muck and marsh border soils. They show a continuous zonation from the open water to the prairie meadows of the terraces. Since they are today almost always either grazed or cut for marsh hay, only fragments are available from which can be pieced together what was originally the vegetation of most of the open valley floor.

In one typical example there are seven distinct zones which may with propriety be recorded here for comparison later with the disturbance communities. Roughly they correspond with the zones described by Sherff (1913) at Skokie marsh but show obvious differences—particularly in the relative importance of the reed-swamp community in the two locations.

The first zone is the open water, usually of some oxbow slough. Where submerged plants are present they are usually species of Myriophyllum, Ranunculus, and Batrachium. Immediately around this zone and exceeding it in extent, a zone of duckmeats *(Lemna trisulca* and *L. minor)* represents the floating-leaved aquatic stage. Beyond this a narrow band of bulrush *(Scirpus validus)* exists, which may be dignified by designation as a separate zone. The first extensive community is the fourth zone dominated by sticktight *(Bidens cernua)* but with prominent representation of touch-me-not *(Impatiens biflora)* and arrowhead *(Sagittaria latifolia)* in the lower interstices. In this zone the water is above the surface for the greater part of the growing season but in the fifth zone organic accumulation has brought the soil level slightly above the water table. This zone, dominated by bluejoint *(Calamagrostis canadensis)*, is probably the most extensive and floristically the richest of these meadow communities. The dominance of Calamagrostis is strikingly uniform, but more careful observation will reveal important and rather extensive societies of reed canary grass *(Phalaris arundinacea)*, *Carex trichocarpa*, and manna grass *(Glyceria grandis)*. Forbs are numerous in this zone,

sunflower *(Helianthus giganteus, H. grosseserratus)*, swamp milkweed *(Asclepias incarnata)*, swamp thistle *(Cirsium muticum)*, water parsnip *(Sium suave)*, red dogwood *(Cornus stolonifera)*, and glaucous willow *(Salix discolor)* are examples of plants reaching above the Calamagrostis, and rough bedstraw *(Galium asprellum)*, *Impatiens biflora*, and marsh bluebell *(Campanula aparinoides)* live below it.

As one approaches the edge of the lowland where outwash or river levees form a slightly more well-drained site the flora begins to change. Here Calamagrostis is joined by meadow rue *(Thalictrum dasycarpum)* and slough grass *(Spartina pectinata)*. Likewise characteristic of this transition zone are Turk's cap lily *(Lilium michiganense)*, bottle gentian *(Gentiana clausa)*, speedwell *(Veronica virginiana)*, cupplant *(Silphium perfoliatum)*, and basil *(Pycnanthemum virginianum)*. But this sixth zone is only a narrow transition to the last zone, the prairie meadow.

This community is usually upon Ray or Wabash soils rather than the muck and marsh border soils upon which the previous zones lie. Drainage is fairly good and the water table is at least three feet below the surface during most of the year. *Andropogon furcatus* is the dominant. It is only on sandy sites that *A. scoparius* appears with its associates, purple love-grass *(Eragrostis spectabilis)* and *Leptoloma cognatum*. Switch grass *(Panicum virgatum)* is another grass which was probably very important in this aboriginal community.

Among forbs there remain several species from the previous zones: *Helianthus giganteus, Thalictrum dasycarpum, Lilium michiganense,* and *Silphium perfoliatum;* but they are joined by a host of new species characteristic of prairies and dry places, among which yellow avens *(Geum strictum)*, ox-eye *(Heliopsis scabra)*, prairie anemone *(Anemone canadensis)*, horsemint *(Monarda fistulosa)*, and wild indigo *(Baptisia leucophaea)* are all conspicuous.

COMMUNITIES OF THE EXPLOITATIVE PERIOD

It was these aboriginal communities that made up the landscape in which the early settlers lived. Between 1840 and 1850 they trickled in slowly but in the second decade the pace increased. By 1861 there were 11,500 persons in Vernon County. With increasing numbers of settlers the area more and more felt the impact of a new, individualistic economy and of new land uses.

The economy of the white settler was largely one of land mining. Along the Mississippi River timber was cut to burn on the river boats and within the area itself there was considerable lumbering and sawmills were run by the many streams. Where scrub or prairie or forest had prevailed before, the land was now plowed and sown with wheat for the high grain prices of the sixties and seventies. On steep slopes the aboriginal communities survived or went forward in natural succession, but intensive grain farming prevailed almost everywhere else. Gullies often developed under this strenuous land use but by

1880 a fatal combination of chinch bug and drought ended the wheat farming and replaced it with beef raising which was, in turn, to be replaced by dairy farming. Eventually more than 50.9 percent of Vernon County farm income came from milk sales. The gullies in the grain fields, now turned into permanent pasture, showed a tendency to heal. This was a more slowly destructive agriculture; it took many years before the inevitable depletion of soil fertility showed in the overgrazed hill pastures. This period of exploitative agriculture which lasted from 1860 until 1934 corresponded to a time when technology had proceeded beyond the primitive Indian methods, which could only slightly modify the natural balance, and had reached a stage where that balance could be completely destroyed. Vegetative retrogression is throughout characteristic of this stage of agricultural technology.

The ways in which the settlers affected the natural communities of the area were many and various. The new land use was based on private exploitation of natural resources. Fence lines were put up and the day of the Indian fire passed. A new monotype of crop land appeared in the area. The natural woodlands were grazed or cut over for timber and then pastured. Even by simply coming onto the land the settlers brought weeds and new plants that changed the aspect of the natural communities.

NEW WOODS TYPES

Red Oak Woods.—The checking of burning was the most important immediate effect of settlement upon the natural vegetation. The scrub grew up into forest after the fires ceased. The writer has spoken to an old settler who could remember scrub not high enough to interrupt the view when, 60 years ago, he hunted deer on the present site of a stand of red oak timber.

Topographically this forest type exists almost anywhere except on the coulee bottoms. It is found on the ridge tops on Clinton silt loam, on the edges on Dubuque, on steep slopes of all exposures with truncated profiles mapped under no series, and at the slope bottoms on the mixed colluvial and sandstone-derived soils of the Boone series. Throughout the area its structure and floristic composition are remarkably uniform; everywhere it gives the impression of a forest 60 or 70 years old.

A typical red oak woods might be located at the head of a draw on the sides of which are clustered numbers of open-grown white oaks, many of them over 200 years old. Age distributions among the red oaks would seem to indicate that they spread upward from the draws. In one woods averages were taken of fifteen trees immediately about the draw, halfway up the slope, and on the upper slope. The figures were 74, 71, and 68 years old, respectively. The present canopy is composed almost exclusively of *Quercus rubra* but a scattering of 60- to 80-year-old *Carya cordiformis, C. ovata, Quercus alba,* and *Juglans cinerea* show that red oak was not the only invader when the fires were checked. In general, white

oak and the hickories are characteristic of the drier uplands, butternut of the moister slopes.

Under the 70 to 90 percent canopy of the red oak is an understory, meager in comparison with that of the maple-basswood type, composed mostly of bitternut and white oak but with considerable admixture of butternut *(Juglans cinerea),* black cherry *(Prunus serotina),* and shagbark hickory *(Carya ovata).* Perhaps the most notable aspect of the understory is the relative unimportance of red oak. An occasional sugar maple *(Acer saccharum)* and red maple *(Acer rubrum)* present here raise the question whether these woods may not be undergoing a type conversion toward the maple-basswood woods.

If a well-developed understory characterizes the maple-basswood community, this woods type is characterized by its well-developed shrub layer. The two most important shrubs are *Corylus americana* and *Cornus femina* (grey dogwood), but species of raspberry and blackberry *(Rubus* spp.) and of gooseberry *(Ribes* spp.) are also conspicuous. For the rest, the shrub layer has occasional individuals of box elder *(Acer Negundo),* plums *(Prunus nigra* and *P. americana),* choke cherry *(P. virginiana),* and *Aralia racemosa* (which, though anatomically herbaceous, functions here as a shrub during most of the growing season, in marked contrast to its habit in the maple-basswood community) together with most of the species which appear in the understory.

One striking feature of this association is the presence of extensive societies of interrupted fern *(Osmunda claytoniana)* which may cover slopes of over an acre. These societies are composed almost exclusively of the one species but at the ground level, underneath the plants, two species of bedstraw *(Galium concinnum* and *G. triflorum)* are prominent, while plants such as *Aralia racemosa* and *Athyrium angustum* var. *rubellum* compete aerially with the Osmunda. Athyrium also competes below the ground as its rootstocks occupy the same top 4 inches as those of the Osmunda.

In the herb layer juvenile individuals of the shrub species are numerically the most important and make up the major part of the ground cover. Nevertheless, several true herbs are conspicuous, notably crane's bill *(Geranium maculatum),* tick trefoil *(Desmodium acuminatum),* enchanter's nightshade *(Circaea latifolia),* hog peanut *(Amphicarpa bracteata),* and wild sarsaparilla *(Aralia nudicaulis).* The *Sanicula trifoliata* of the maple-basswood community is replaced here by *S. marilandica, Polygonatum pubescens* by *P. biflorum.*

Xeric Oak Woods.—Within the area are many south and west slopes on rough broken land or Dubuque soils where conditions were too dry for the red oak community to develop after fires ceased. Here there grew up a faciation of the oak-hickory formation adapted to a drier environment.

Dominance here is shared by several species of oak, black oak *(Quercus velutina),* jack oak *(Q. ellipsoidalis),* and bur oak *(Q. macrocarpa),* but an occasional *Q. rubra* shows an affinity with the red

TABLE 4. Line transect counts of various species in the red oak association communities.

Columns grouped as: Original (1–4), Disturbed (5–9), Recovery (10–13).

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
HERBS													
Acalypha virginica							1						
Acer Negundo	1										1		
Ac r rubrum							3	25					
Actea rubra					1								1
Adiantum pedatum			2								2		
Agrimonia grypsosepala			2										
Amphicarpa bracteata	7	13	14	12	10	1	14	8	2	4		18	19
Anemone quinquefolia var. interior	3	3											
Antennaria plantaginifolia				3			2	1					
Apocynum androsaemifolium	2	7									1		
Aralia nudicaulis	3	1	22										
Aralia racemosa													1
Arisaema triphyllum			9	3									
Asclepias phytolaccoides			1						1				
Aster paniculatus												3	1
Aster sagittifolius			1	1	3	3	1	2	1	1			1
Athyrium angustum var. rubellum		2	10	13			3	9				7	4
Bidens frondosa							6						
Botrychium virginianum			1								1		
Carex pennsylvanica*		5	9										
Carex rosea*	1												
Carya cordiformis	1		11	4			2		2	1		4	7
Carya ovata			1										
Caulophyllum thalictroides			1										
Celastrus scandens			9										
Chenopodium album							1						
Circaea latifolia	15	3	15	10		10	22	35	3	3		1	3
Cornus alternifolia											1	1	
Cornus femina	21	18	5	5						14	15	5	5
Cornus rugosa				1									
Corylus americana	10	7	8	5					1	2	9		
Cryptotaenia canadensis				2			1						
Desmodium acuminatum	15	9	9	1					1				2
Desmodium nudiflorum			7	3									1
Dioscorea villosa	3				3				1				2
Epilobium glandulosum var. adenocaulon					3								
Erigeron philadelphicus							1						
Erigeron ramosus						1			5		3		
Eupatorium rugosum												2	2
Fragaria vesca							1		7				
Fragaria virginiana			2								13	3	1
Galium concinnum	7	4	16		5	12	1		7	30	34		
Galium triflorum		1	2	10			12	5				23	16
Geranium maculatum	15	14	27	20			1				12		
Geum canadense						1			2	6	1	2	
Helianthus strumosus	3												
Juglans cinerea	1		1										
Lappula virginiana								5	4	1			
Maianthemum canadense					1								
Nepeta Cataria								1	1				
Osmorhiza Claytoni				4	4					2	7		
Osmunda Claytoniana	11	7		6			2						
Oxalis europaea				2			4	4					
Parietaria pennsylvanica					4		4						
Parthenocissus vitacea	2	2								9			15
Phlox divaricata				2									
Phryma leptostachya		1	1	4	1		20	4		1	1		5
Pilea pumila							126	69					
Plantago major			1			1	5	19	8		1		1
Polygonatum biflorum			2										
Polygonum Convolvulus							5						
Polygonum Persicaria					14		20	31					
Potentilla simplex		1		1			3		2	1		4	3
Prunella vulgaris						1	1	2	22	2			1

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
HERBS (Cont.)													
Prunus nigra			2										
Prunus serotina		1	28	3							6	1	2
Prunus virginiana			11	2							1		
Pteridium latiusculum	2												
Pyrola elliptica									2	1			
Quercus alba	2										1	1	
Quercus rubra		1	1	2			2	1	1	4	3	1	1
Rhus Toxicodendron	11												
Ribes Cynosbati		1	7	9			2		2	6	2	1	
Rosa blanda	1						1			3			
Rubus hispidus	8	20											
Rubus idaeus var. strigosus				1		1				3	6	15	
Rubus occidentalis		6	3	2					12	11		6	
Rubus sp.	2	6	11	24		1				3	18	4	5
Sambucus canadensis				1		1		1					
Sanicula gregaria			8										
Sanicula marilandica	2	1	1								1		
Smilacina racemosa	9	4	3	1		1					7		
Solidago canadensis												14	8
Stachys tenuifolia			3										
Steironema ciliata			1										
Stellaria media						6		8					
Taraxacum officinale							5	24					
Thalictrum dioicum			8										
Trifolium repens						2		1	34			1	
Trifolium grandiflorum			2	5							1		
Uvularia perfoliata	4	3	12	21									
Viburnum Lentago			1										
Vicia americana											1	5	
Viola cucullata	1					6	5	14	5				
Vitis riparia				8							1	6	14
TREES													
Carya cordiformis			1	1									
Carya ovata				1			2						
Prunus serotina			1										
Quercus alba			1					1		1	6	2	1
Quercus rubra	11	9	6	6	4	7	6	5		3	3	4	7
UNDERSTORY													
Carya cordiformis		3	2										
Juglans cinerea	2	1		1									
Prunus serotina	2										2		2
Quercus alba	1	1	2	3	1	1	2			1		3	2
Quercus rubra			1		3	4				2		2	
Ulmus americana	1												
SHRUBS													
Acer Negundo	1			1							2	2	2
Aralia racemosa	1	3	3										
Carya cordiformis	2		4	2									
Carya ovata	1												
Cornus alternifolia			3								1	1	
Cornus femina	15	3	2	4						22	14	4	2
Cornus rugosa			5										
Corylus americana	21	7	3	8						19	15		
Lonicera Morrowi												1	2
Populus tremuloides										1	1		
Prunus nigra			2										
Prunus serotina	1										4		2
Prunus virginiana			2	1									
Quercus alba	1		1	1									
Ribes americanum													2
Ribes Cynosbati										3	1	1	
Rosa blanda	1	1	1							1			
Rubus idaeus var. strigosus			2								7	6	19
Rubus occidentalis			1										5
Rubus sp.			6	6						4	9	2	4
Viburnum Lentago			2										
Vitis riparia												2	2

*No attempt was made to record the number of grasses and sedges in the disturbed and recovering communities.

Notes on communities surveyed:

1, 2 } Ridge woods in LaCrosse County.
3, 4 } Ridge Woods in Vernon County.
5   In cowpath; badly disturbed.
6   Canopy nearly intact; slight north slope.
7   Canopy not much disturbed; moist site.
9   Dry site with much sod cover; canopy disturbed.
10, 11 } Out of pasture, five years under contract.
12, 13 } Continuous sheep pasturing ended eight years ago; undisturbed since.

oak type. The shrubs both in importance and in
species composition are rather conspicuously remi-
niscent of this woods type, although here is seen more
of rough dogwood *(Cornus rugosa)*, *Zanthoxylum
americanum*, thorn apple *(Crataegus* sp.), and New
Jersey tea *(Ceanothus americanus)*.

The herb layer closely resembles that of the red
oak association in species composition but the meso-
phytes have been lopped off and slightly more xeric
types like panic grass *(Panicum praecocius)*, sedge
(Carex Muhlenbergii), pussytoes *(Antennaria plan-
taginifolia)*, *Pycnanthemum virginianum*, *Monarda
fistulosa*, evening primrose *(Oenothera muricata)*,
and *Heliopsis scabra* take their place.

Structurally these woods are the simplest of any
so far described; the community is usually only a scat-
tering of trees with a dense scrub beneath.

NEW SPECIES

The most subtle effect which white men have had
upon the woods community is the addition of new
species. It is not only the weeds which fill the
natural woods clearings or the ubiquitous *Poa pra-
tensis* which spreads even into the undisturbed woods.
Man has brought in many plants which have become
important interlopers in the "aboriginal" communi-
ties. Both box elder *(Acer Negundo)* and poison ivy
(Rhus toxicodendron) were absent originally from
the red oak community of which they are now an
important part. Ecologically they are "native."
Highbush cranberry *(Viburnum trilobum)* and Mor-
row's honeysuckle *(Lonicera Morrowi)* are well es-
tablished in some woods where they could not be
found at the beginning of the century. One area in
particular, adjacent to a nursery, is resplendent with
many exotics such as Ohio buckeye *(Aesculus glabra)*,
chestnut *(Castanea dentata)*, and black walnut *(Jug-
lans nigra)*—not originally common in this area.

PASTURING

Den Uyl et al. (1938) trace the successive steps in
the degeneration of a forest under grazing. The
first stages are marked by the disappearance of
shrubs and by grazing injury to herb species. In
the transition stage tree reproduction is destroyed and
the canopy begins to open. Weeds and grass appear
in the herb layer. If grazing persists the canopy
opens as some trees die, others become stagheaded, and
reproduction is absent. In the "open park stage"
there is a very nearly continuous sod cover which
affords the most unfavorable conditions for tree re-
production. As trees die the pastured woods ap-
proach the final stage with scattered trees, the last
dying remnants of the complete woods community.

In the Coon Valley Area most of the woods have
been grazed only into Den Uyl's transition stage,
probably because the region has been settled little
more than half as long as Indiana. Should grazing
continue it can be expected that the later stages will
show as conspicuously here as they do now in Indiana.

Pastured Red Oak Woods.—Pasturing has three
main effects upon the red oak woods which illustrate

fairly well the effects which soon arrive upon the
pasturing of any woods type.

1. The more delicate members of the community
are soon exterminated or reduced to isolated relicts.
Since most juvenile individuals of tree species are
included in this category, pasturing means an ef-
fective end to tree reproduction. This effect is well
illustrated in the sample transects taken of grazed
red oak woods (Table 4). Not only do species such

FIG. 3. Red oak woods type. Area to the left of fence
has been grazed, area to the right has not been grazed.
Note disappearance of tree reproduction and shrub
layer, invasion of grass, and opening of canopy under
grazed conditions.

as bellwort *(Uvularia perfoliata)*, tick trefoil *(Des-
modium acuminatum)*, jack-in-the-pulpit *(Arisaema
triphyllum)*, and *Sanicula marilandica*, present in all
ungrazed red oak transects, completely disappear, but
juvenile individuals of woody species were reduced
from 253 in four ungrazed transects to 46 in four
grazed ones (and 25 of these 46 were seedlings of
Acer rubrum on one transect). The shrub layer prac-
tically disappears through browsing and deficient re-
production decimates the understory. Thus in three
out of four grazed transects there are absolutely no
shrubs and the 19 understory individuals of the un-
grazed transects contrast neatly with the 12 of the
grazed. Although it does not show up conspicuously
in the transects there seems to be a definite tendency
for thorny trees and shrubs such as *Ribes Cynosbati*,
crabapple *(Pyrus ioensis)*, and *Crataegus* spp. to ex-
pand at the expense of other less well-protected
species.

2. Grasses and sedges present when grazing begins
greatly increase and other grasses such as *Poa pra-
tensis* invade vigorously, particularly on dry spots
where the canopy has opened. Point quadrat* counts
show that the ratio of grasses and sedges to other
higher plants was 1:25 in the ungrazed woods and
5:1 in the grazed type.

3. Some woods annuals and inconspicuous peren-
nials increase materially and annual weeds begin to
invade the disturbed community (see Table 3). On
the drier sites healall *(Prunella vulgaris)*, dandelion
(Taraxacum officinale), pussytoes *(Antennaria plan-*

* See section "A Note on Method."

taginifolia), white clover *(Trifolium repens)*, and daisy fleabane *(Erigeron ramosus)* are important. In moist, shaded places enchanter's nightshade *(Circaea latifolia)*, chickweed *(Stellaria media)*, and lady's thumb *(Polygonum Persicaria)*, all appear.

FIG. 4. Red oak woods grazed. Note lack of shrub layer and presence of grass in herb layer. The white oak in the center is probably over 150 years old and was grown under relatively open conditions. The other trees, which are 60 to 80 year old red oaks, are forest grown.

There are interesting increases in two annuals, rich-weed *(Pilea pumila)*, ordinarily a plant of river bottoms in dense shade, and *Parietaria pennsylvanica* which thrives exposed to sun and dryness in the rock crevices of the juniper flats. Yet with all these new species, ground cover in grazed woods is only 48.7 percent of the cover in ungrazed (Table 5).

TABLE 5. Percent frequency of various species found in ungrazed and grazed red oak woods as determined from point quadrat studies.

Ungrazed	Grazed	
Non-grassy species.... 96.6	PART 1.	
Grassy species........ 3.4	Non-grassy species....17.9	
Density index........100.0	Grassy species......82.1	
	Density.............71.2	
	PART 2.	
	Non-grassy species....14.3	
	Grassy species.......85.7	
	Density.............26.2	
	TOTAL	
	Non-grassy species....16.9	
	Grassy species.......83.1	
	Density.............48.7	

Maple-Basswood Type Grazed.—When the maple-basswood community is grazed much the same processes take place as in the red oak community but they are here modified by special conditions, particularly of light. Grass invades here, too, but it is not as important as *Carex rosea* which simply spreads moderately under the still intact canopy. The shrub layer —unimportant in undisturbed maple-basswood woods —now disappears completely and practically all the characteristic herbs disappear at once. Of all the complex and populous herb layer, only a few, such as *Sanicula gregaria* and honewort *(Cryptotaenia canadensis)* remain. The herb layer now consists largely

of *Circaea latifolia* and *Pilea pumila*, important here as in the grazed red oak woods, and, characteristic of this exploitative community, white snakeroot *(Eupatorium rugosum)* and blue violet *(Viola cucullata)*. In view of the poisonous effect of Eupatorium, pasturing in these woods probably has a deleterious rather than a beneficial effect upon livestock.

Minor Woods Types Grazed.—The elm river bottom community is usually grazed heavily so that now the majority of the sites are in the open park stage with a continuous layer of sod, no shrubs, no tree reproduction, and very few herbs. The vernal herbs of the original community seem to persist best because they pass through most of their seasonal cycle before the grazing begins, although trampling undoubtedly does injure them. What shrubs do remain are thorny: prickly ash *(Zanthoxylum americanum)*, *Crataegus punctata*, and gooseberry *(Ribes missouriense)*. Moisture and shade-loving weeds like *Pilea pumila, Polygonum Persicaria, Parietaria pennsylvanica*, and lady's sorrel *(Oxalis europaea)* come into the herb layer. Of the rich and varied river bottom community only the vernal aspect and an occasional

FIG. 5. Heavily grazed maple-basswood type in transition stage. Note complete absence of underbrush, weedy white snakeroot in ground cover and sun flecks where the canopy is opening up as the trees die. There is four times as much light here as in ungrazed type in Fig. 1.

Carex albursina, white grass *(Leersia virginica)*, or waterleaf *(Hydrophyllum appendiculatum)* remain.

The least vulnerable of all the woods communities is the white pine consociation, for it is only the nimblest of cows which can negotiate its steep bluffs. Although there exist several areas where cattle have had access to this consociation for considerable time, there has been no very remarkable change in these places except in the introduction of weeds like *Parietaria pennsylvanica, Stellaria media*, bladder campion *(Silene latifolia)*, and goosefoot *(Chenopodium hybridum)*. Rare endemics have persisted, even in the face of grazing, thanks to their inaccessibility.

Under pasturing the black oak community undergoes much the same changes as the red oak community. Delicate species such as *Arisaema triphyllum, Desmodium acuminatum, Thalictrum dioicum*,

and *Campanula americana* disappear along with tree reproduction; grasses invade and spread, particularly Kentucky bluegrass *(Poa pratensis)*, and Canada bluegrass *(P. compressa)* which often crowd out the more mesic species of Carex *(C. rosea, C. Muhlenbergii, C. mirabilis)*; and a number of species of pasture weeds, *Taraxacum officinale, Ambrosia artemisiifolia,* plantain *(Plantago major)*, and mullein *(Verbascum Thapsus)* begin to invade. Xeric species present like *Antennaria plantaginifolia, A. neodioica,* and *Monarda fistulosa* may actually increase in area. Structurally the chief feature of this exploitative community again is the complete disappearance of the shrub layer.

Most of the grazing is done by dairy cattle but an occasional farmer keeps sheep and pastures them in his woods. In this case the disturbance community brought about differs markedly from that when grazing is done only by dairy cattle. Sheep browse on the shrubs and low trees and they will eat the weeds which cows refuse. Consequently a woods grazed by sheep soon has its shrub layer completely destroyed except for a rare individual of gooseberry *(Ribes* sp.), and the herb layer disappears to leave *Parietaria pennsylvanica,* nettle *(Urtica gracilis)*, or bull thistle *(Cirsium lanceolatum)* to mark the passing of a numerous host.

Goat Prairies Grazed.—Because of their steep slopes, most of the goat prairies within the area are protected from grazing, but an occasional one on a gently sloping knoll will be intensively pastured. On grazing *Poa compressa* and *P. pratensis* invade along with some of the drier pasture weeds such as *Verbascum Thapsus,* fleabane *(Erigeron ramosus), Oenothera muricata, Ambrosia artemisiifolia,* and cinquefoil *(Potentilla simplex)*. Under grazing the clump grasses, Andropogon and Sorghastrum, quickly disappear but *Bouteloua curtipendula* with its sod habit tends to remain. A sprinkling of forbs, lead plant *(Amorpha canescens), Aster sericeus,* Pasque flower *(Anemone patens* var. *Wolfgangiana),* and purple prairie clover *(Petalostemum purpureum)* all linger, but if grazing continues it will probably not be long before they are pushed out by the two Poas.

The effect of grazing upon the marsh meadows will be treated below.

LUMBERING

Red Oak Woods.—In many places the red oak woods have been cut without being pastured. This initiates a new exploitative community. The effects of cutting are threefold: (1) the species of the canopy are removed and the structure thus artificially simplified, (2) the more tender species cannot compete under new conditions of exposure to sun and wind and are (3) replaced by expanding species, some of which existed under the original canopy and some of which have invaded since the disturbance.

Most striking is the expansion of the shrub layer, particularly of *Corylus americana* though *Cornus femina* expands as well. Vines present in the red oak woods such as woodbine *(Parthenocissus vitacea),*

river grape *(Vitis riparia),* and bittersweet *(Celastrus scandens)* expand in importance, and root sprouts of *Populus grandidentata* and *P. tremuloides* appear in the hazelbrush. Also significant is the abundance of tree reproduction with red and white oak and bitternut hickory much the most conspicuous. Some of the herbs remain; the most conspicuous are a number of ferns, *Osmunda Claytoniana, Athyrium angustum* var. *elatius* (here this and *A. angustum* var. *rubellum* seem to be merely ecological forms of what is genetically the same thing), *Adiantum pedatum* and some of the more xeric seed plants of the original community such as *Galium concinnum, Anemone virginiana,* and *Veronica virginiana.* There are also some new invaders which fall naturally into two categories, one of disturbance weeds *(Erechtites hieracifolium,* fireweed, *Ambrosia artemisiifolia,* and *Erigeron ramosus),* and the other of xeric forbs from other communities *(Aster sagittifolius, Solidago canadensis,* and *Monarda fistulosa).*

Maple-Basswood Woods.—When the maple-basswood community is cut over the same general effects occur as in the red oak woods but here different species are involved. Shrubs develop rapidly but this time they are *Rubus idaeus* var. *strigosus, Staphylea trifolia, Corylus cornuta,* and juvenile individuals of *Carya cordiformis, Juglans cinerea,* and *Ulmus fulva.* The luxuriantly growing relict ferns here are *Pteretis nodulosa, Dryopteris Goldiana, Athyrium angustifolium,* and *A. angustum* var. *elatius* which seems to be characteristic of cut-over areas. *Laportea canadensis, Campanula americana, Polymnia canadensis,* and *Phlox divaricata* are relicts from among the seed plants. Together with these relicts a host of plants, weeds, and characteristic herbs of drier or more open communities than the maple-basswood woods come in as disturbance indicators. *Celastrus scandens* appears along with *Impatiens pallida, Prunus virginiana,* hairy brome *(Bromus purgans),* giant ragweed *(Ambrosia trifida),* cow parsnip *(Heracleum lanatum),* figwort *(Scrophularia lanceolata),* and elderberry *(Sambucus canadensis).* Structurally these cut-over communities are usually little more than a dense tangle of shrubs and tall herbs with the tolerant plants growing in the lower, shaded interstices. Because the environment varies from that of *Solidago canadensis,* in the drying sun, to that of *Impatiens pallida,* in the shade, there is found in this exploitative community a surprisingly large number of ecologically diverse species.

DISTURBED MARSH AND PRAIRIE MEADOWS

The marsh meadows of the river bottoms are almost universally exploited either for hay or for pasture, although in many years they are too wet for any use. Either haying or grazing will change the aspect of the meadow, but the effect of grazing is far more drastic.

Haying.—Cutting for hay when pursued over a number of years will keep the large forbs—particularly the many composites—from setting seed and will tend to decrease root reserves. Thus haying

FIG. 6. Marsh meadow cut for hay on left side of fence and pastured on other side. Note compression of zones of succession in pasture. The area of bluegrass dominance extends over most of the pasture and replaces the Calamagrostis of the hay meadow.

gradually replaces these species with the aggressive Calamagrostis and the sedges. Eventually a hay meadow loses practically all its forbs and Calamagrostis dominance is practically complete.

Grazing.—Pasturing a meadow has a much more profound effect upon the vegetation than does cutting for hay. Around the sloughs the open water and Lemna zones are comparatively unchanged but the next zone is modified by the increased importance of Scirpus and the introduction of cattail *(Typha latifolia)*. The presence of *Polygonum Persicaria* shows plainly the effect of pasturing in this zone. The Bidens-Impatiens zone has the two principal dominants remaining but in decreased importance since here they are joined by rush *(Juncus effusus)*, bulrush *(Scirpus atrovirens)*, sedges *(Carex hystericina* and *C. vulpinoidea)*, *Pilea pumila*, *Polygonum Persicaria*, mint *(Mentha arvensis)*, horehound *(Lycopus americanus)*, and monkey plant *(Mimulus ringens)*. Occasionally blue vervain *(Verbena hastata)* is a sign of grazing disturbance. On the outward edge of this zone there is a band of low Calamagrostis which represents the only example here of that species so abundant in the ungrazed meadow. All of these zones described are compressed in width and stunted in development under grazed conditions. Outward from this narrow band lies the true pasture portion of the meadow corresponding to the Calamagrostis and prairie meadow zones of the ungrazed meadow. This is usually dominated by *Poa pratensis* though *Agrostis alba* is important and in places assumes dominance. *Trifolium repens* is the frequent legume and weeds characteristically include *Verbena hastata*, blue lobelia *(Lobelia syphilitica)*, thoroughwort *(Eupatorium perfoliatum)*, and *Prunella vulgaris*. In general the composition and structure of the vegetation tends strongly to approach that of upland pastures.

UPLAND PASTURES

This community has been artificially created from forest or scrub. Most pastures found today are old

and established, but from a few newer stump pastures it is possible to imagine these areas directly after they were cleared and first put under grazing. *Poa pratensis* is very rapid in invading and soon establishes dominance. Yet, within these Poa-dominated communities there still exist relicts of the old forest community. Some of the more persistent are: May-apple *(Podophyllum peltatum)*, *Viola cucullata*, *Geranium maculatum*, *Claytonia virginica*, and wood anemone *(Anemone quinquefolia* var. *interior)*. Lobelia spicata, pussytoes *(Antennaria neodioica)*, and mouse-ear chickweed *(Cerastium vulgare* var. *hirsutum)* are characteristic weeds of these new pastures. As the pastures approach middle age the relict species die out and are replaced by the codominants, *Poa pratensis* and *Trifolium repens*, with some *Poa compressa* on the drier spots. What weeds exist are not abundant and include only such species as *Verbascum Thapsus*, bull thistle *(Cirsium lanceolatum)*, and yarrow *(Achillea Millefolium)*.

EROSION COMMUNITIES

Pastures.—In a hilly country like that of the Coon Valley Area removal or disturbance of the vegetative cover means accelerated erosion, which decreases the soil-nutrient supply and impairs soil moisture relations. This, in turn, again disturbs the vegetation and causes more severe soil erosion. Thus, once started, the accelerating cycle is difficult to halt and the vegetation becomes more and more impoverished. In pastures weeds come in abundantly, first the more noxious perennials like *Verbena hastata*, *Verbena urticaefolia*, Canada thistle *(Cirsium arvense)*, sour dock *(Rumex acetosella)*, and Indian tobacco *(Lobelia inflata)*, and then a host of annuals of which *Ambrosia artemisiifolia*, creeping spurge *(Euphorbia maculata)*, crabgrass *(Digitaria sanguinalis)*, *Erigeron ramosus*, and *E. annuus* are typical. Within the pasture gullies on the raw subsoil are three-seeded mercury *(Acalypha virginica)*, American pennyroyal *(Hedeoma pulegioides)*, catnip *(Nepeta Cataria)*, and horseweed *(Erigeron canadensis)*. With continued erosion even this meager covering of annual weeds will disappear.

Woods Erosion.—Within a woods erosion is not so immediately drastic even though it may be heavily pastured. The first effect is the removal of all the forest relicts which have managed to survive under moderate grazing. Then the more moisture-loving of the weedy species, such as *Circaea latifolia*, *Pilea pumila*, and *Polygonum Persicaria*, diminish in importance or are completely forced out by the oncoming grasses and drought-resistant weeds like *Acalypha virginica*, *Plantago major*, and *Potentilla norvegica* var. *hirsuta*. In the gully bottoms where moisture is more often immediately available the moisture-demanding species will remain, but owing to frequent washes their continued existence must of necessity be precarious.

COMMUNITIES OF THE RECOVERY PERIOD

Fortunately these exploitative communities do not represent the last and final effect of man upon the

vegetation of Coon Valley. As the problem of soil erosion became more pressing there were hopeful signs. Some farmers had known strip cropping in the old country and they brought these soil-conserving methods which they showed to their skeptical neighbors. Checking the trend toward soil depletion, the acreage of alfalfa in Vernon County rose from seven acres in 1899 (Becker, 1920) to 2,560 in 1927 and 12,620 in 1934. But still what was needed was the social framework around which the Valley agriculture could work with the consciousness of a balanced nature. Answering this need the United States Soil Erosion Service (forerunner of the present Soil Conservation Service) entered the Valley in 1933. Soon there were close to 44,000 of the watershed's approximately 90,000 acres under contract and plans were being made for a land use which would keep the soil on the land. Of the 18,000 acres of cropland, 1,236 were turned into pasture and 117 to hay. Vernon County alfalfa acreage reached 35,080 acres in 1937. Before this time there had been less than 2,000 acres of woods protected from grazing; to this the Soil Conservation Service added over 10,000 acres. This represented a new economy of cooperation and a new attitude toward the land just as the soil mining economy of the settlers, themselves, advanced beyond the hunting economy of the red man. With it came a multitude of new successions, growing up around protected woods, renovated pastures, and protected gullies. As the age of exploitative agriculture was characterized by vegetative retrogression so was this period characterized by the abundance of progressive secondary successions. The communities arising under this land use may be called recovery communities.

PROTECTED RED OAK WOODS

When grazing ceases in the red oak woods a number of processes immediately set in which within five years have become plainly visible. Most important is the reappearance of the shrub layer. This shades the ground and crowds out the grass thus making room for tree reproduction. But the shrub layer which now returns is not that of the original red oak woods. Under the less favorable conditions, briars (Rubus idaeus var. strigosus, Rubus occidentalis, Rubus § Eubatus) have to a large extent replaced the hazelbrush and dogwood of the ungrazed red oak, and the amount of replacement seems to be greater with the intensity and damage of the grazing, more with sheep, less with dairy cattle. The sod cover is slow to break up, particularly when the canopy has been disturbed, but as the shade becomes greater it soon is forced to relax its hold. Two of its first competitors are hog peanut (Amphicarpa bracteata) and Galium concinnum which form small societies directly replacing the sod and setting the stage for the return of other woods species.

Characteristic of this recovery community are many species of Solidago and Aster which are able vigorously to compete with the grass cover. As recovery proceeds those true woods species which may have survived under grazing, including Smilacina racemosa, Parthenocissus vitacea, Athyrium angustum var. rubellum, and Geum canadense soon begin to crowd out these composites and the few weeds that are left (Prunella vulgaris, Ambrosia artemisiifolia, and Sonchus arvensis). A glance at the transects (Table 4) and their comparison with those of the grazed and ungrazed red oak woods gives the essential features of the community.

PROTECTED MAPLE-BASSWOOD WOODS

In main outlines the recovery of the maple-basswood type proceeds similarly except that here there is no revival of the shrub layer. The grass which has not been well established under this comparatively dense canopy soon disappears and is replaced by species of Solidago and Aster or by the expanding reliefs of the ungrazed woods. There is often present a good representation of the original herb cover, Osmorhiza Claytoni, Circaea latifolia, Carex laxiflora, C. pennsylvanica, C. albursina, Sanguinaria canadensis, Sanicula gregaria, and Melica mutica, and

Fig. 7. Protected maple-basswood type, ungrazed 5 years. Note recovery of forest floor vegetation, relict grass patches, and absence of shrubs. Tree reproduction is just becoming established and is not vigorous here as under red oak dominance.

Fig. 8. Shrubs invading pasture after one year's cessation of grazing. Note zonation (1) perennial herbs, particularly Canada goldenrod, (2) sumach and hazelbrush, (3) aspen.

a quick recovery can be predicted. Reproduction of *Acer saccharum, Tilia americana,* and *Carya cordiformis* are all entirely adequate. The transects give the main characteristics of this community (Table 2).

RENOVATED PASTURES

Overgrazed and eroded pastures have been reclaimed by renovation or, when the slope was too steep, simply by removing the cattle. Pasture renovation, a method developed in this southwestern portion of Wisconsin, involves fertilization and the introduction of legumes such as the sweet clover *(Melilotus* spp.), alfalfa *(Medicago sativa),* or red clover *(Trifolium pratense).* It helps in pasture recovery both through raising the fertility level and through increasing the organic matter content of the soil. The results are shown in the point quadrat studies (Table 6). Not only is ground cover more complete

TABLE 6. Percent frequency of various species in adjacent renovated and unrenovated pastures as shown by point quadrat studies.

Not Renovated		Renovated	
PASTURE A			
Poa pratensis	46.2	Poa pratensis	58.5
Poa compressa	20.3	Poa compressa	19.5
Trifolium repens	8.4	Trifolium repens	11.3
Taraxacum officinale	0.7	Melilotus spp.	6.2
Rumex acetosella	1.4	Ambrosia artemisiifolia	2.1
Polygonum aviculare	1.4	Taraxacum officinale	2.1
Digitaria sanguinalis	21.0	Cichorium Intybus	0.5
Ambrosia artemisiifolia	0.7		
Density	96.9	Density	136.4
PASTURE B			
PART 1			
Poa pratensis	85.8	Poa pratensis	73.9
Poa compressa	9.7	Poa compressa	17.5
Digitaria sanguinalis	3.9	Melilotus spp.	6.0
Euphorbia maculata	0.6	Panicum sp.	2.1
		Erigeron sp.	0.4
Density	96.9	Density	146.3
PART 2			
Poa pratensis	73.0	Poa pratensis	76.0
Poa compressa	10.9	Poa compressa	14.0
Digitaria sanguinalis	12.1	Melilotus spp.	7.0
Trifolium repens	1.8	Ambrosia artemisiifolia	2.9
Euphorbia maculata	0.6		
Cyperus filiculmis var.			
macilentus	0.6		
Density	103.1	Density	106.9
TOTAL: PARTS 1 AND 2			
Poa pratensis	79.7	Poa pratensis	74.8
Poa compressa	10.3	Poa compressa	16.0
Digitaria sanguinalis	8.1	Melilotus spp.	6.4
Trifolium repens	0.9	Ambrosia artemisiifolia	1.2
Euphorbia maculata	0.6	Panicum sp.	1.2
Cyperus filiculmis var.		Erigeron sp.	0.2
macilentus	0.3		
Density	100.0	Density	126.6

in the renovated pastures but *Poa pratensis* dominance is more complete and the weeds are reduced. The *Digitaria sanguinalis* and *Euphorbia maculata* prominent in the unrenovated pastures do not show up in the renovated quadrats and both *Ambrosia trifida* and *Erigeron canadensis* are eventually eliminated. The rather consistent absence of *Verbena hastata* from renovated pastures and its abundance in the unrenovated may be an index of the change brought about through renovation.

ABANDONED PASTURES

The abandoned pasture or one lightly grazed presents another recovery community, often with zonation toward the neighboring woods. When grazing is lessened *Monarda fistulosa, Pycnanthemum virginianum, Solidago canadensis,* and *Aster paniculatus* appear in the midst of the sod cover. With complete cessation of grazing there are abundant shoots of *Corylus americana, Cornus femina,* and the two species of sumach *(Rhus glabra* and *R. typhina).* Under grazing there is often a zonation with this group of shrubs to the woodward side of the pasture. Palatability differences eliminate the hazel and dogwood to the advantage of the sumach. Beyond this zone there is usually a zone dominated by aspen but with white, red, and black oaks and shagbark hickory coming up under its shade. Beyond this remains only the woods which is usually of the red oak type.

Herb cover varies within these shrub and tree zones. Thus the shrub zone is accompanied by a number of xeric herbs of which *Solidago canadensis, Monarda fistulosa, Pycnanthemum virginianum, Helianthus strumosus,* and *H. divaricatus* are representative. Within the zone of aspen there are most of the drier woodland herbs, *Galium concinnum, Thalictrum dioicum, Anemonella thalictroides* (usually found in these woods-pasture transitions), *Amphicarpa bracteata, Veronica virginiana, Geum canadense,* and *Smilacina racemosa.*

GULLY RECOVERY COMMUNITIES

As a result of the many changes in land use brought about by the United States Soil Conservation Service, erosion and run-off have decreased. Today many gullies are rapidly healing and are being covered with protecting vegetation. The many zones of the healing gully form a series of recovery communities.

Pasture Gullies.—The first zone in the open gully bottom, where the running water provides a very unstable environment, is occupied almost entirely by annual weeds, *Erigeron canadensis, Ambrosia artemisiifolia, Bidens frondosa,* and *Acalypha virginica.* With them may be found *Agrostis alba, Juncus macer, Rumex crispus, Asclepias syriaca,* and *Salix amygdaloides* or *S. discolor.* Grazing pares down this community and leaves only annual weeds.

The second zone lies just above the first on the sides of the gully. It is usually dominated by grassy species, most often by *Agrostis alba.* With it come many perennial weeds, *Verbascum Thapsus, Oenothera muricata, Rumex acetosella,* and a number of

shrubby species, *Rubus § Eubatus, Ribes Cynosbati,* and *R. missouriense, Prunus virginiana,* and the often planted black locust *(Robinia pseudoacacia).* Grazing usually reduces this shrub and removes the very effective tangle of horsetail *(Equisetum arvense)* which is rather commonly present in this zone.

The third and last zone is usually on the upper part of the gully sides where it grades into the surrounding vegetation. This zone very often has a complete sod covering though in that sod there may be interruptions caused by groups of Equisetum or by shrubs. *Solidago canadensis, Monarda fistulosa,* and *Veronica virginiana* are herbs characteristic of this zone, and elderberry *(Sambucus canadensis)* is a shrub which marks the stage of stabilization. In the pasture this zone simply does not exist but is replaced by the communities of the depleted and eroded pasture. Beyond this third zone in the ungrazed gully there is a transition into the woods or surrounding grassland.

Woods Gullies.—Under woods conditions the recovery of a gully shows something of the same zonation but the species here are changed. In the first stage the weeds are *Oxalis europaea, Pilea pumila, Prunella vulgaris, Bidens frondosa,* and *Cerastium vulgatum* var. *hirsutum,* but there are also a number of woods species such as *Amphicarpa bracteata, Parthenocissus vitacea,* and *Cystopteris bulbifera.* On the sides grow *Prunus virginiana, P. pennsylvanica, Campanula rotundifolia, Aquilegia canadensis,* and more *Parthenocissus vitacea.* The third zone gradually leads into the ordinary vegetation of the forest type. Owing to the lack of grass and sod cover, healing in a woods gully is, in general, not so rapid as in an open one.

SUCCESSIONS IN THE VALLEY

There can be no doubt, after reading surveyor's reports and hearing the recollections of old settlers, that scrub oak barrens throughout the area have given way to red oak woods in succession forward from a disclimax community. The red oak type, itself, may be regarded either as the regional climax or as a rather stable subclimax which will, however, eventually give way to the regional climax, the maple-basswood woods. Since the Coon Valley Area is in a transition region between the mixed hardwood climax on podzolic soils to the north and the oak-hickory formation on grey forest soils to the south, it would appear that this line of tension is a delicate one and that small factors would tend to swing it either way. Nevertheless, the writer is of the opinion that much of the area now occupied by the red oak woods type will eventually come to be occupied by the maple-basswood woods. The reasons may be briefly summarized as follows:

1. Under cover of the red oak canopy there is little reproduction of the dominant species. Instead the chief juvenile species are white oak, bitternut hickory, butternut, basswood, and sugar maple. This would seem to indicate that here red oak is not able to reproduce under its own shade and is replaced by trees more typical of the maple-basswood type.

2. In many particularly favored portions of the red oak woods, mostly about ravines, there already exist subcommunities resembling the maple-basswood type. The canopy here is mostly *Tilia americana* and *Juglans cinerea;* beneath it are such shrubs and plants as *Staphylea trifolia, Asarum canadense* var. *acuminatum, Hepatica acutiloba, Panax quinquefolium,* and *Osmorhiza Claytoni.* These subcommunities within the red oak woods indicate that at least in some areas succession has already taken place toward the maple-basswood type.

3. The eastern portion of Vernon County has much the same climate as does the western. In spite of this, the dominant forest type in the western part is the red oak, while in the eastern part the maple-basswood type prevails. This can be explained by the historical accident that Indian settlement and consequent burning was probably greater about the Mississippi than about the Kickapoo. The conclusion would seem to be that in the east where disturbance has not been so great the forests have reached the climatic climax; in the west they may do so if left undisturbed.

4. This protection through historical accident is paralleled by a protection through topographic peculiarities. The present sites of the maple-basswood type almost uniformly possess some advantage of exposure or position which would protect them from fires sweeping over the ridges or up the coulee bottoms. Thus the majority of the other woods sites, the red oak sites, were, up to seventy years ago, exposed to fire, a factor which never disturbed the other sites. The prevalence of this type at present can be explained then by the practically simultaneous cessation of the factor which prevented its coming into being. The present red oak woods, having begun together, are now all in approximately the same stage of succession.

The second succession within the area is one deriving from the bare rock and shallow soils of the goat prairie. Some idea of the first stages can be had from the zonation around a typical goat prairie. Immediately about the edges and invading among the prairie plants is a first zone of *Rhus glabra,* summer grape *(Vitis aestivalis), Ceanothus americanus, Celastrus scandens,* and *Parthenocissus vitacea* with an occasional scattered *Betula papyrifera.* This soon gives way to the second zone which is an almost impenetrable tangle of *Cornus femina* and *C. rugosa* with some Vitis, Celastrus, Parthenocissus, and honeysuckle *(Lonicera Sullivantii).* This, in turn, leads to a zone where *Quercus macrocarpa* and *Carya ovata* are coming in with most of the foregoing species as undergrowth plus arrow-wood *(Viburnum affine* var. *hypomalacum)* and nannyberry *(V. Lentago).* This last zone grades insensibly, in time, probably, as it does in space, into the black oak community already described. It is probable that the seventy-year-old black oak woods, with accumulation of organic mat-

ter and soil development, passes into the red oak woods. And this, it seems, tends toward the maple-basswood type. It is interesting to note that this proposed succession agrees substantially with that worked out by Pool, Weaver, and Jean in Nebraska (1918).

In the midst of this dynamic picture of community relations within the area it is important to present a more static scheme of the present vegetation. Thus, on the dry crest of a steep southwest slope, the vegetation is usually of the goat prairie type. About it, on south or west slopes, the xeric black oak woods typically remains. On many of these drier sites it is probable that no organic accumulation will bring about succession until the geologic cycle has reduced these sidehills to gentle slopes. Thus these early stages of the succession may be said to be physiographically determined.

West, north, and east slopes and woods on the ridges are typically red oak woods. It is only an occasional northeast slope which shelters the maple-basswood type. But, in view of the facts presented above, it is probable that this last progression in succession is one biotically determined and proceeding within observable time.

It is obvious that the zones of the marsh meadow represent successional stages of which the Calamagrostis stage is probably the longest in time as it is also in breadth of space occupied. Up to this stage the hydrarch succession is probably biotically determined, but the transition between Calamagrostis and prairie meadow is not entirely a matter of organic accumulation. A glance at the soil under these prairie meadows shows that they rest on deposited sediments. Evidently sedimentation is necessary to bring about the transition from Calamagrostis to Andropogon.

The grazed marsh meadow has a parallel succession, but it seems that, in the early stages at least, the succession proceeds more slowly under grazing, since the organic matter increment to the soil is usually much smaller under pasture conditions.

The succession brought about in a woods by continued grazing has already been discussed. This is a biotically determined succession. After five years recovery communities show a tendency to revert to the aboriginal, ungrazed types, but from this it cannot be stated definitely that succession will go on indefinitely until the original vegetation has been restored. In many cases erosion has taken place under grazing and this soil loss may stabilize the succession at some level lower than the aboriginal community. Thus many of the introduced weeds may now become permanently characteristic of these communities.

The cut-over areas and the abandoned pastures quite naturally undergo a progressive succession, apparently toward the aboriginal type. The cut-over areas seem to return but in eroded pastures, where retrogressive succession has taken place, the vegetation may never—except in the very long run—reach the level which it had originally attained. Gullies tend to go through the successional stages indicated by their marginal zones but, in recovery, they will probably never become identical with the surrounding wood or grassland, in the midst of which they maintain a ravine community characterized by additional water, less sunlight, and less soil nutrients. It is only physiographic change which eventually obliterates the ravine community by rounding off the steep gully slopes.

A NOTE ON METHOD

The vegetative surveys were made using two distinct procedures. In sod vegetation, or one with large numbers of grassy plants, the inclined point quadrat method was used. This involves the use of the point quadrat machine, an apparatus by which ten needles can slide at a 45-degree angle from a point above the vegetation down to the ground surface. Each time any plant part is touched by a needle point a "hit" is recorded for that species. The total number of hits for any species compared with the grand total number of hits is an index to the proportion of ground covered by that species (Tinney, Aamodt, and Ahlgren, 1937). In woods, where vegetation was of clumps or of single plants rather than of sod-forming grasses, the vegetative survey was accomplished by means of line transects. These involved counting the individual plants of each species which touched the vertical plane above a 100-yard line extended through the woods at the soil surface. In counting the plants, they were divided into structural categories—herbs, shrubs, understory, and trees. The results (Tables 2 and 4) are equivalent to the number of individuals of each species found in a given area.

In the course of the study attempts were made to determine some of the factors which make for the different structure and composition of the various communities examined. Measurements were made of evaporation and light intensity. These are shown in Tables 7 and 8, respectively.

The evaporation readings were made with porous

TABLE 7. Relative evaporation from selected environments during August, 1939, using the maple-basswood woods type as base.*

Community	Relative Evaporation
Maple-basswood type I.............	1.000
II.............	1.036
Red oak type	
Hillside.....................	1.298
Ridge.....................	1.250
Ratio $\frac{\text{Pastured red oak}}{\text{Unpastured red oak}}$	1.782
Goat Prairie.................	3.885
Prairie Meadow.................	1.529
Marsh Meadow.................	0.645
Ratio $\frac{\text{Pastured Meadow...}}{\text{Unpastured Meadow.}}$	1.708
Cutover Maple Basswood...........	0.758

*Absolute evaporation is not given since the measurements were made with porous clay tubes, not with Livingston evaporimeters.

The evaporating surfaces were in all cases placed approximately 8 inches above the surface of the ground.

TABLE 8. Frequency distributions of illumination intensities in foot candles from selected environments.

Illumination Intensity	RED OAK				MAPLE-BASSWOOD		
	Hillside Ungrazed	Ridge Grazed	Ridge Osmunda Society	Ridge Ungrazed	Ungrazed I	Ungrazed II	Grazed
8 – 15 F.C.*..	...	...	...	...	2	..	...
16 – 31 F.C....	...	...	2	...	6	10	...
32 – 63 F.C....	2	5	6	3	7	4	...
64 – 127 F.C....	5	8	4	9	1	2	2
128 – 255 F.C....	4	2	1	2	1	1	9
256 – 511 F.C....	4	4	..	1	..	1	2
512 – 1024 F.C...	3	1	..	2	..	1	4
Over 1024.......	1	4	1	3	2	1	3
Modal Intensity .	102	83	53	90	34	18	192
Mean Intensity..	210	180	71	168	48	56	270

*F.C. = Foot Candles.

elay cups calibrated with each other under constant conditions. Since the readings were not made with standard equipment the observations are good only for comparisons among themselves.

The light intensity readings were made with a Weston Camera Light Meter and a G-M Exposure Light Meter. They were taken in various environments at constant intervals along a 50-yard line.

DISCUSSION

It was one purpose of this study to find plant indicators of the processes of land deterioration, erosion, and recovery which we have noted. Although it has not been possible to do just this, the communities attendant on these various processes do show conspicuous differences.

In a woods there is first a disappearance of the more tender natural species, as the destructive cycle begins, then an influx of such weeds as *Polygonum Persicaria, Parietaria pennsylvanica,* and *Prunella vulgaris,* and lastly grasses enter with the more difficultly eradicable weeds such as *Cirsium lanceolatum, C. arvense, Verbascum Thapsus, Verbena hastata,* and *Lobelia inflata.* Recovery brings first an onrush of composites, particularly Aster and *Solidago* spp., and then a prominent expansion of the remaining relicts and a recovery of the shrub layer. In pastures overgrazing and attendant erosion bring *Euphorbia maculata, Digitaria sanguinalis,* and large quantities of *Ambrosia artemisiifolia.* Grassy dominance seems to pass towards *Agrostis alba* as the topsoil is washed away. With recovery these species disappear and the more valuable *Poa pratensis* follows *P. compressa* in reassuming dominance.

Incipient gully erosion shows a transition from the ordinary pasture or woods vegetation to perennial herbs and shrubs on the gully sides and annual weeds on the bottom. Recovery is the reverse of this and dominance generally passes from annuals through perennials to woody plants. Good indicators of gully stabilization are *Solidago canadensis, Monarda fistulosa,* and *Veronica virginiana* on the sides, *Sambucus canadensis* and *Ambrosia trifida* on the bottom. From their frequent importance in the first and second stages of gully erosion, respectively, *Phleum pratense* and *Equisetum arvense* might be suggested as species worth a trial as vegetative cover on bare gully sides. Amphicarpa and Parthenocissus are often found in woods gullies and might be useful for planting here; under favorable conditions Amphicarpa forms sizeable societies which are undoubtedly valuable ground cover. The advantages of Rubus, Sambucus, and *Salix* spp. in vegetative control are already well known.

The evaporation readings show results which may be significant although the readings include only the last three weeks of August. One striking feature is the uniformity of evaporation in the two replications of the red oak and the maple-basswood woods. High evaporation is a characteristic of the goat prairies which is apparently not duplicated in the lowland prairie. Lowest evaporation of all occurs under the dense herb cover of the marsh meadow and the cutover maple-basswood community.

The contrast between the plant population of the grazed and ungrazed woods is paralleled by contrasts in environmental conditions. Evaporation increases when woods are grazed and the soil reaction rises as less organic matter is added to the soil. With the gradual opening of the canopy the average illumination intensity increases.

The environmental differences between the two principal woods types are conspicuous. The red oak woods is higher in evaporation and illumination than the maple-basswood type and its soil reaction is more acid. Within the red oak woods the environment of the Osmunda societies is characterized by less illumination than the remainder of the woods and a more acid soil reaction.

SUMMARY

This study has purposed to show the relation between land use and plant succession within the Coon Valley Soil Conservation Area. The history of the area has been paralleled with concomitant plant communities initiated by and following upon three general schemes of land use.

In the first period Indians used repeated ground fires in their hunting economy. This reduced the exposed forest to a mixed oak and hazel shrub. On protected slopes and in coves a rich community dominated by maple and basswood escaped the fire. On the creek bottoms there were areas of elm-dominated woods and on steep, north-facing slopes there were occasional areas of a northern woods type dominated by white pine. There were small prairies scattered about the area, on the ridges, on dry southwest slopes, and on the valley terraces. In the bottoms marsh meadows, largely of Calamagrostis, occupied moist open spots.

The first white settlers stopped the Indian fires and set up a new exploitative land use of their own. From the scrub of the Indians sprang the shrubfilled red oak woods, now the prevailing woods type of the area, and a woods of mixed xeric oaks. In crop

and pasture land new communities appeared as white agriculture extracted wheat, beef, and finally milk from the land. Pastured woods lost tree reproduction and their tender species and were invaded by grass and weeds. In these woods evaporation increased, insolation was greater, and the soil reaction was higher. Pastures cut from the woods passed from the woodland-relict stage of the stump pasture, through the blue grass and white clover of the high pasture, to the crabgrass and weeds of the depleted and eroded pasture. Gully erosion started in woods and pasture bringing new retrogressive successions of weeds and grasses. The marsh meadows were disturbed by haying and grazing; even the isolated goat prairies often felt the impact of pasturing.

The arrival of the United States Soil Conservation Service in the Valley was the beginning of a new land use which is, even yet, only developing. Grazing was discontinued in many woods, depleted pastures were renovated, and gullies were fenced off from grazing and planted to soil-conserving vegetation. The results are apparent after only five years of cooperative effort. Weeds disappear from the woods, the shrub layer reappears, hosts of composites come in and the woods apparently tends to its original state as the sod cover breaks up. The renovated pastures show improved ground cover and the crabgrass disappears. Gully communities are transformed to metastable ravine communities.

The regional succession seems to be prairie, to brush, to xeric oak woods, to red oak woods, to maple-basswood woods, but it is not at all certain that this succession will go to completion on all sites. Evaporation readings show that this succession tends toward moister conditions. The maple-basswood woods is more shaded and its soil more nearly neutral than that of the red oak type.

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ECOLOGY OF SAND BEACHES AT BEAUFORT, N. C.

A. S. PEARSE, H. J. HUMM, and G. W. WHARTON
Duke University, Durham, N. C.

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ECOLOGY OF SAND BEACHES AT BEAUFORT, N. C.

INTRODUCTION

The finer materials of the earth's crust are continually sorted out by gravity, winds, and water movements. The finest particles make clays or muddy oozes in situations where there is little or no movement in transportive fluid media. Sand occurs where winds, waves, or currents have carried and deposited bits of silica, shell, or other hard substances. Ordinary sand is 2,100 times as heavy as air, but only 2.5 times heavier than water; so waves and currents can carry larger and heavier bits than can wind (Olsson-Seffer 1910). Dunes are eolian deposits; on the whole they consist of smaller grains of sand than neptunian strands along wave-beaten shores. There is zonal segregation along the shores of a lake or on a marine beach where tides ebb and flow twice daily. In general the coarsest particles are found where there is greatest activity in water. There large bits of sand or even pebbles are rolled about and deposited. Above or below the violent surgings of littoral waves and currents there are fine particles. At high tide mark these are mixed with a varied assortment of flotsam and jetsam. Below low tide mark they grow gradually finer until, beyond the carrying activities of cyclonic wave movements, they gradually merge with the soft oozes and red clay deposits which occur outside continental shelves on bottoms in the open sea.

A marine sandy beach seems like an inhospitable place for plants and animals to become established. On a rocky, wave-beaten headland, where storms rage and intertidal areas are exposed alternately to cool, surging water and hot or cold desiccating air, there may be an abundant biota of attached seaweeds, hydroids, barnacles, clams, etc. The rocks may be literally carpeted with living things. On the other hand a shifting, sandy beach is usually without much apparent life. There may be seen an occasional scuttling crab, a school of little fishes wiggling into the shallows, or a solitary sandpiper drilling holes with his long beak. In general a sandy shore seems to be a barren, clean place—admirable for bathing, but unpromising as a habitat where a biologist may collect or study animals. But appearances are deceiving. Marine littoral sands swarm with plant and animal life. Furthermore, many species show most interesting and peculiar adaptations for existence in a medium that is continually overturned and rearranged, that is deficient in oxygen and contains much carbon dioxide (Germann 1938), and where size of particles controls pore volume and hence permeability and rate of percolating water. If particle size of sand grains is reduced 10 times, permeability is reduced 100 times (Carman 1938). Yet such beaches swarm with living psammobionts, or sand dwellers.

On sand beaches along the shores of freshwater lakes more psammobionts live in wet regions exposed to air than in those that are submerged (Pennak, 1940), and most of them are found in the upper 3 cm. The same is true of many plants and animals that are indigenous on marine sand beaches, but there are also characteristic types that dig down a meter or more and some of these remain continually in their burrows. Some psammobionts such as sand dollars (Mellita) and isopods (Chiridotea) are quite flat and live on or very near the surface of sand. Waves slide over without carrying them away. However, most dwellers in sand beaches escape the force of flowing water by burrowing. Nematodes and small annelids remain near the surface of the sand. Copepods have similar habits. Wilson (1935) showed that many of what he termed "terraqueous" copepods are strikingly adapted for life among sand granules which have pore spaces, but are unable to live among flat, tightly packed shell fragments. Certain molluses (Weymouth 1920), crustaceans (Garstang 1897, Mac Ginitie 1932, 1934, 1937, 1938), and spatangoids, though they burrow, remain close to the surface; others descend to considerable depths and have special means (siphon tubes, pumps, etc.) for respiration and feeding. Besides the animals that live in sand there are bottom animals that hunt on the surface. These include flounders, sea robins, top minnows, portunid crabs, ostracods (Tressler 1940), etc. On intertidal beaches such insects as tiger beetles and flies (Greene 1923) breed and forage for food. At night ghost crabs (Ocypode) and beach "fleas" (Talorchestia; Smallwood 1903) come out of their burrows and swarm along sandy shores.

THE BEAUFORT REGION

The Duke University Marine Laboratory on Piver's Island at Beaufort, N. C., is located at 34° 43′ N. and 76° 41′ W. Situated on an island, it gives easy access to several sounds, banks (long, coastal, sandy, dune-covered islands), and estuaries (Fig. 1). Seven stations were established around the mouth of Beaufort Inlet where observations were made each week throughout the summers of 1939 and 1941. Other observations were also made at irregular intervals at all seasons.

Gutsell (1931) published data concerning variations in salinities and temperatures at Piver's Island. These were based on daily observations from September, 1924 to October, 1928. Maximum and minimum salinities (ppm.) for the whole period were as follows: January, 35-14; February, 35-16; March, 34-15; April, 35-15; May, 35-23; June, 37-22; July, 38-21; August, 38-21; September, 37-6; October, 35-

14; November, 35-16; December, 37-20. Maximum and minimum water temperatures (°C) were: January, 15-3; February, 22-6; March, 22-6; April, 23-12; May, 27-16; June, 30-21; July, 32-23; August, 33-23; September, 32-21; October, 36-12; November, 26-8; December, 23-4. Of course the stations studied by the writers were subjected to somewhat less variation in temperature and salinity, as they were closer to the open ocean, but Gutsell's figures give a general idea of conditions in estuaries at Beaufort. We have taken many temperatures during summer months in, on, and above sand beaches. These will be given later in this paper.

The following climatic data are published in the records of the United States Weather Bureau (Marvin 1933) for Beaufort, N. C., for 28 years. Average precipitation (1872, 1896-1930) in inches is: January, 3.92; February, 4.12; March, 3.87; April, 3.36; May, 3.40; June, 4.78; July, 6.16; August, 5.53; September, 4.80; October, 4.38; November, 2.74; December,
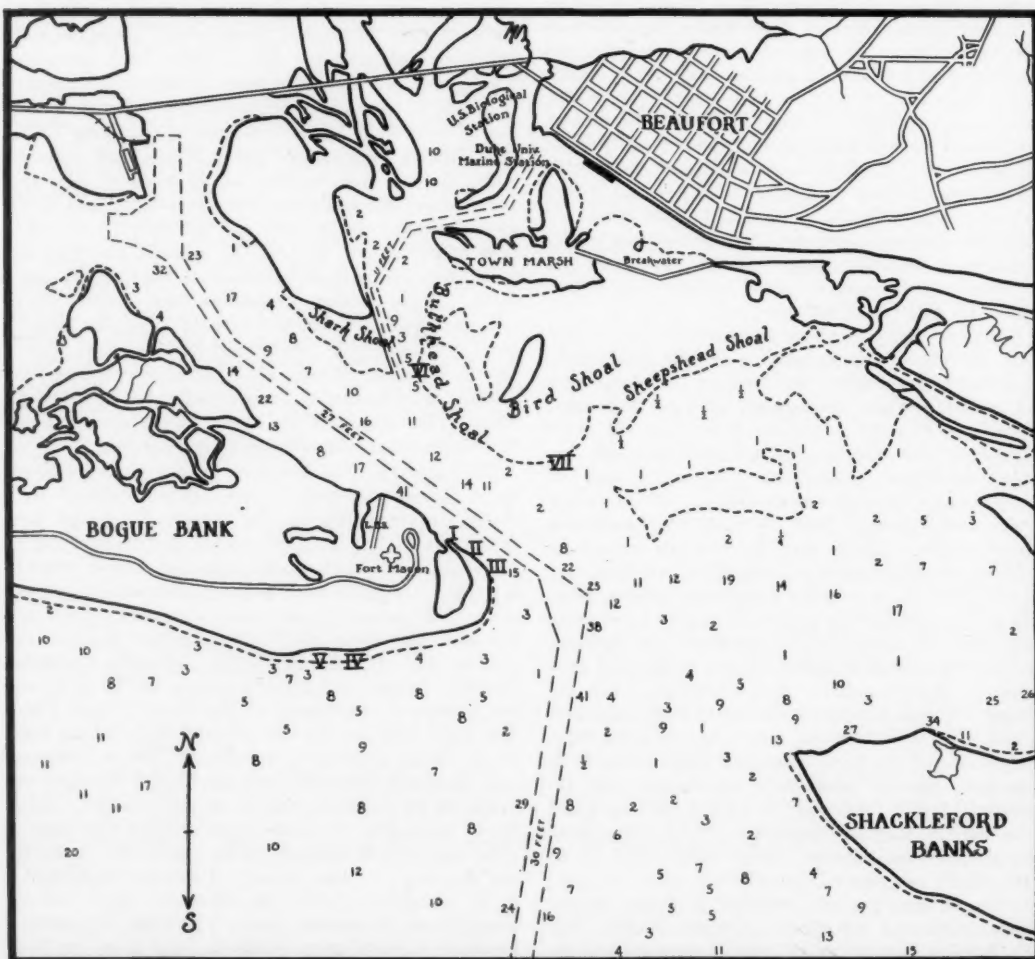
FIG. 1. Map of the Beaufort Harbor, with observation stations indicated in Roman numerals and depths in feet.

4.40; total annual, 51.46. Average snowfall at Beaufort is given as: January, 0.4; February, 0.3; March, 0.2; December, 0.4; total annual, 1.3 in. Average monthly, and average maximum and minimum air temperatures (°F) have been as follows: January, 47.9:56.3-39.9; February, 48.2:56.4-40.3; March, 53.8:62.2-45.7; April, 60.9:68.9-53.4; May, 69.5:76.6-62.6; June, 76.3:82.9-70.0; July, 79.8:85.7-73.7; August, 79.5:85.7-73.2; September, 76.0:82.8-69.4; October, 66.6:74.2-58.7; November, 56.6:64.6-48.5; December, 48.8:57.0-41.1; annual average, 63.7:71.1-56.4. Prevailing winds during most of the year are from the southwest, but during September, October, and November are northeasterly. Average date of last killing frost in spring is March 9, and of first in autumn, December 9. The growing season therefore averages 269 days.

The biota of the Beaufort region is particularly interesting because a considerable number of north- and south-ranging species of plants and animals are found there. Some of these are permanent residents, others are brought in by storms from the Gulf Stream, which is only about 25 miles offshore.

METHODS

Seven stations (Fig. 1, I-VII) were selected for study. These were all near the entrance of Beaufort Harbor, as follows:

I. Along ship canal near Fort Macon, on a gently sloping beach 150 feet from Station II.

II. Along ship canal near Fort Macon, on a beach of medium slope 150 feet from Station III.

III. Along ship canal near Fort Macon, on an abruptly sloping beach.

IV. Near Fort Macon on beach of open ocean; slope gradual; bar and lagoon alongshore.

V. Near Fort Macon on beach of open ocean; slope gradual; bar and lagoon alongshore; 300 feet from Station IV.

VI. Bird Shoal, on large, flat bar which was covered at high tide; slope abrupt to adjacent channel.

VII. Sheepshead Shoal on large, flat bar which was covered at high tide; slope gradual to channel.

At intervals observations were also made on Shark Shoal, Guthrie Shoal, Shackleford Bank, and Shipstake Shoal (Fig. 1). Hauls with trawls and dredges were made in various places in sounds and offshore in the open ocean. Bottom samples were taken by using a diving hood.

In the investigation of marine sand beaches it is difficult to make field observations accurate and comparable from day to day, for conditions vary with direction of winds, height of tides, precipitation, and variations in other environmental factors.

Various methods and pieces of equipment were employed in collecting data. The most important of these were as follows:

Walking along Beach.—Especially after a strong onshore wind, many plants and animals were left stranded but at any low tide things might be picked up that were not often secured in any other way.

Spades.—Digging was a very satisfactory source of specimens. By watching for the openings of burrows or peculiarities in sandy surfaces, animals were often turned out.

Rakes.—An ordinary metal garden rake was fitted with a semicircular bar to which a net was attached (Fig. 2). When the teeth were dragged through the sand below water, crabs and other animals were caught.
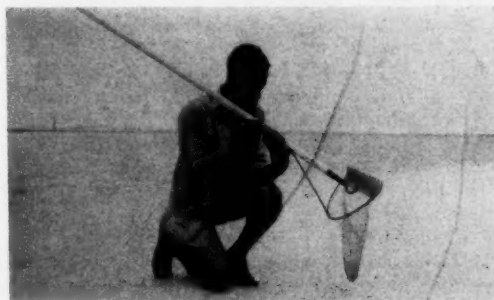

FIG. 2. Reginald with rake net.

Salve Boxes.—Flat metal salve boxes that had a capacity of 17.5 cc. were filled with sand and carried into the laboratory for examination. In the summer of 1939 duplicate samples were shaken separately with sea water; the water was filtered; the filtrate was then washed off into a small volume of water and the contained animals were counted under a binocular dissecting microscope. During 1941 duplicate samples were examined by successively placing small portions of sand on a glass plate under a binocular microscope and teasing particles across the field until all the organisms of a sample had been counted. These methods were satisfactory for fairly large animals (copepods, ostracods, amphipods, snails, nematodes, foraminiferans, some other protozoans, etc.) but were of course inadequate for counting small algae and bacteria.

Sieves.—Duplicate samples were sifted through square sieves with coarse meshes and through round sieves with fine meshes. In 1939 coarse sieves had a capacity of 15 liters and the bottom was covered with galvanized wire screen having three meshes per centimeter. In 1941 coarse sieves had a capacity of 6.5 liters and two meshes per centimeter. Fine sieves in 1939 and 1941 had a capacity of 6.5 liters and their screens had six meshes per centimeter. Screens were placed on the bottom and filled with beach sands by using a spade. The contents were then washed through into the water alongshore. At times screens were used by wading out and dipping up sand from the bottom and sifting it through. They were also used to sift sand brought up from deep waters by using a diving hood and bucket on a line.

Diving Hood.—Up to depths of about seven meters a diving hood was used in collecting samples from sandy bottoms. A diver descended, filled a bucket

with his hands or with a short-handled spade, and the sample was then drawn to the surface.

Seine.—A 30-ft. minnow seine which had a 1 cm. (½ in.) mesh was hauled alongshore and the animals caught were counted.

Dredge.—A steel-framed dredge with a rectangular opening was hauled over the bottom at intervals. It had an opening 40 by 15 cm. and a bag a meter long with meshes at the apex 6 mm. wide.

Trawl.—Otter trawls which had spreads of 3.5 meters and 10 meters were hauled at various depths on sandy bottoms in the ocean off Ft. Macon.

Tow Net.—A few towings were made and examined, but systematic routine catches were not made.

Water Samples.—Water samples for determinations of salinity, oxygen, pH, etc., were taken with a Kammerer sampling bottle which had a capacity of one liter. Samples from sand were taken through a sieve at the end of a brass tube and drawn into a 150 cc. glass receiver with stop cocks.

Temperatures.—Readings were taken with a mercury-filled bulb thermometer, and at times in deep water with a Negretti-Zambra deep sea thermometer.

Salinities.—Three Geiner hydrometers and Knudsen's tables were used in determining salinities. At times titrations with silver nitrate were made.

Ionizations.—Three La Motte colorimeters were used to determine pH's.

Oxygen.—The Winkler method was used in determining the amount of oxygen present in water samples.

Particle Size.—Dried sand samples were sifted through standard soil sieves to determine amounts of particles of various sizes (U. S. Dept. Agr. Tech. Bull. No. 170).

Humus.—The organic content of sand samples was determined on 1 gram samples by oxidizing with a chromic acid and sulphuric acid solution, adding phosphoric acid and diphenylamine indicator, and titrating with a ferrous ammonium sulphate solution until blue color changed to gray-green.

Calcium.—Dry sand samples were weighted, treated with hydrochloric acid, washed with distilled water, dried, and weighed again in order to determine the amount of lime. Soluble particles were mostly shell fragments, but occasional fish bones and other calcareous substances also contributed small amounts.

PHYSICAL CONDITIONS IN BEAUFORT SAND BEACHES

Particle Size.—Largest grains of sand tend to accumulate at about low tide mark. Results of several determinations made in 1939 are shown in Table 1.

Humus.—A few determinations of humus content of sand from various levels were made during the summer of 1939. The results were:

Ft. Macon, outside: 0.02-0.07; ave. of 4 samples, 0.05%.

Ft. Macon, inside: 0.03-0.07; ave. of 5 samples, 0.05%.

Sheepshead Shoal: 0.09-0.15; ave. of 4 samples, 0.12%.

TABLE 1. Particle size of sand on beaches at Beaufort, N. C. Figures indicate percentages. Stations are shown in Figure 1.

Stations	Level	No. of samples	Size in millimeters				
			+1	1-0.5	0.5-0.25	0.25-0.1	-0.1
I, II, and III	Drift L.	2	0.1	0.1	1.7	95.1	3.1
	H. T. M.	2	0.0	0.4	18.9	80.4	0.4
	½ T.	4	0.2	0.7	33.4	65.3	0.4
	L. T. M.	2	0.7	2.1	19.0	77.3	1.1
	Below L. T.	2	0.6	2.5	19.4	76.5	1.1
IV and V	Drift L.	8	0.4	3.0	19.4	75.1	2.0
	H. T. M.	11	0.1	0.5	25.6	73.2	0.5
	½ T.	11	0.6	3.0	23.3	76.5	1.1
	L. T. M.	8	14.5	13.4	13.0	55.2	2.4
	Below L. T.	1	0.8	4.8	40.0	54.2	0.1
VI and VII	Above Water	6	1.4	4.9	46.5	54.9	0.2
	Pool	4	7.6	3.8	23.1	54.7	0.9
	L. T. M.	4	1.2	2.1	18.7	77.6	0.4
	Below L. T.	4	1.6	3.9	23.8	69.7	0.3
Shipstake Shoal	H. T. M.	2	1.0	2.0	20.4	76.0	0.6
	½ T.	2	0.2	0.4	1.6	92.2	5.8

TABLE 2. Calcium in sand beaches at Beaufort, N. C. Figures indicate number of observations and percentages.

Locality	Drift L.	H.T.M.	½ T.	Pool	L.T.M.	1 m. deep
Ft. Macon, outside	4-4.3	6-1.8	5-3.9	.....	6-15.8	.....
Ft. Macon, inside	.....	1-4.9	3-3.42	.....	1-6.61	.....
Sheepshead Shoal	.....	2-3.7	3-5.2	4-5.5	2-5.2	3-6.7

In the section on the plants of sand beaches it is shown that more bacteria are present at high tide mark than at lower levels. This is perhaps because there are more organic substances than below.

Calcium.—Our limited observations indicate that lime in sand beaches increases from high tide mark and is greatest toward low tide mark and below (Table 2). Where there is greatest wave action there are often most shell fragments near low tide mark. The high percentage at drift line on the beach toward the open sea (Ft. Macon, outside) was perhaps due to shell fragments thrown up by storms.

Temperatures.—During the summer of 1939 temperature records were as follows:

Ft. Macon, outside (Stations IV, V)

Air: max., 26.0; min., 24.0; ave. of 7 observations, 24.9°C.

Ocean surface: max., 26.8; min., 24.5; ave. of 10 observations, 26.5°C.

Ocean, 3-6.5 m. deep: max., 26.7; min., 24.5; ave. of 4 observations, 26.1°C.

Sand: 1 observation, 26.0°C.

Ft. Macon, inside (Stations I, II, III)

Air: max., 27.0; min., 23.5; ave. of 5 observations, 25.8°C.

Ocean surface: max., 29.5; min., 24.6; ave. of 8 observations, 26.5°C.

Ocean, 0.5-6.5 m. deep: max., 27.5; min., 24.6; ave. of 4 observations, 25.1°C.

Sand: 1 observation, 30°C.

Sheepshead Shoal (Station VII)

Air: max., 27.0; min., 20.5; ave. of 9 observations, 25.4°C.

Ocean surface: max., 30.6; min., 24.0; ave. of 14 observations, 27.5°C.

Ocean, 0.5-2.3 m. deep: max., 26.5; min., 24.1; ave. of 2 observations, 25.3°C.

Sand: 1 observation, 25.0°C.

Pool: 1 observation, 28°C.

During the summer of 1941 temperatures were taken regularly when collecting was done on beaches. The results were as follows:

Ft. Macon, outside (Stations IV, V)

Air: 23.4-28.1; ave. of 7 observations, 26.2°C.

Ocean surface: 22.7-29.5; ave. of 9 observations, 26.4°C.

Sand, H. T. M., 1 in. deep: 22.7-39.5; ave. of 7 observations, 31.0°C.

Sand, H. T. M., 6 in. deep: 23.2-37.0; ave. of 7 observations, 30.1°C.

Sand, 'tween tides, 1 in. deep: 22.6-34.5; ave. of 6 observations, 28.0°C.

Sand, 'tween tides, 6 in. deep: 22.0-33.0; ave. of 6 observations, 27.2°C.

Sand, L. T. M., 1 in. deep: 22.8-32; ave. of 6 observations, 26.9°C.

Sand, L. T. M., 6 in. deep: 22.8-30.2; ave. of 6 observations, 26.4°C.

Ft. Macon, inside (Stations I, II, III)

Air: 23.1-27.4; ave. of 4 observations, 24.5°C.

Ocean surface: 24.0-24.6; ave. of 4 observations, 24.3°C.

Sand, H. T. M., 1 in. deep: 24.0-35.1; ave. of 4 observations, 28.3°C.

Sand, H. T. M., 6 in. deep: 24.1-33.0; ave. of 4 observations, 27.0°C.

Sand, 'tween tides, 1 in. deep: 25.0-28.8; ave. of 4 observations, 26.7°C.

Sand, 'tween tides, 6 in. deep: 24.8-28.8; ave. of 4 observations, 26.1°C.

Sand, L. T. M., 1 in. deep: 23.0-28.0; ave. of 3 observations, 25.3°C.

Sand, L. T. M., 6 in. deep: 23.5-26.2; ave. of 3 observations, 24.8°C.

Bird and Sheepshead Shoals (Stations VI, VII)

Air: 24.0-29.0; ave. of 9 observations, 27.5°C.

Ocean surface: 23.8-30.0; ave. of 9 observations, 26.5°C.

Sand, H. T. M., 1 in. deep: 25.0-34.0; ave. of 9 observations, 26.7°C.

Sand, H. T. M., 6 in. deep: 24.0-31.0; ave. of 9 observations, 27.4°C.

Sand, 'tween tides, 1 in. deep: 27.5-32.0; ave. of 7 observations, 29.7°C.

Sand, 'tween tides, 6 in. deep: 25.0-31.0; ave. of 7 observations, 27.7°C.

Sand, L. T. M., 1 in. deep: 26.5-30.2; ave. of 6 observations, 29.3°C.

Sand, L. T. M., 6 in. deep: 24.5-30.3; ave. of 6 observations, 27.8°C.

These data indicate that during summer days air above sandy ocean beaches is usually cooler than littoral waters. On the Fort Macon beaches, which are not completely covered with water at high tide, temperatures in sand are lower at lower levels; those at a depth of six inches in sand average lower than those at one inch. On the Bird and Sheepshead Shoal beaches, which are completely covered by tides, temperatures in sand are lower on the highest levels and higher on those below, but temperatures at 1 inch in sand were higher than those at 6 inches.

On November 8 and 9, 1941, when stiff southwesterly breezes prevailed and tides were low. In late afternoon temperatures at time of low tide were as follows:

Ft. Macon, outside (Station IV)

Air: 14.8; ocean surface: 17.8°C.

Sand, H. T. M.: 1 in. deep, 17.5; 6 in. deep, 17.8°C.

Sand, 'tween tides: 1 in. deep, 17.2; 6 in. deep, 16.4°C.

Sand, L. T. M.: 1 in. deep, 17.9; 6 in. deep, 17.5°C.

Water in lagoon near L. T. M., 17.2°C.

Ft. Macon, inside (Station II)

Air: 15.3; ocean surface: 18.2°C.

Sand, H. T. M.: 1 in. deep, 19.0; 6 in. deep, 17.7°C.

Sand, 'tween tides: 1 in. deep, 15.8; 6 in. deep, 15.7°C.

Sand, L. T. M.: 1 in. deep, 18.0; 6 in. deep, 18.3°C.

Bird Shoal (Station VI)

Air: 16.0; ocean surface: 18.5°C.

Sand, highest level: 1 in. deep, 17.6; 6 in. deep, 17.8°C.

Sand, 'tween tides: 1 in. deep, 18.4; 6 in. deep, 19.0°C.

Sand, L. T. M.: 1 in. deep, 16.0; 6 in. deep, 17.8°C.

At greater depths in water or in sand beaches temperature variations are less extreme and changes are slower than those near the surface.

Salinity.—Salinities on all the beaches studied at Beaufort were rather high throughout summer seasons. In 1939 results were as follows (ppm. means parts *pro mille*, or grams per liter):

Ft. Macon, outside.

Ave. of 4 at surface of ocean 34.85 ppm.

1 at 3.5 m., 34.99; 1 at 5.5 m., 34.88; 1 at 6.5 m., 34.36 ppm.

Ft. Macon, inside.

Ave. of 5 at surface 33.98 ppm.

1 at 5.5 m., 34.63; 1 at 6.5 m., 33.96 ppm.

In sand at L. T. M.: 1 in., 34.02; 6 in. 33.65 ppm.

Bird and Sheepshead Shoals.

Ave. of 4 at surface, 34.23 ppm.

In sand: 3 at 1 in. deep 34.00; 2 at 2 in. deep, 34.30; 3 at 3 in. deep, 34.59; 4 at 4 in. deep, 34.04; 1 at 5 in. deep, 33.53; 2 at 6 in. deep, 34.59; 1 at 7 in. deep, 34.18 ppm.

All salinities were not much below that of the open ocean.

Oxygen.—Three observations on water from the surface of the open ocean off Fort Macon Beach showed 4.96, 4.20, and 5.04 cc. of oxygen per liter. On the beach outside Fort Macon in sand near the water's edge at a depth of 1.5 in. there was, 0.0 cc.; at 1.5 in. in sand and 1 in. under water, 0.0; 1 in. under water and 2 in. under sand, 0.0. On the beach inside the cape at Fort Macon (Station II) surface water contained 4.88 and 5.28 cc. of oxygen per liter; at water's edge and 1 in. in sand, 0.83; water's edge and 3 in. in sand, 1.50, 0.0, 0.83, 0.82; water's edge and 6 in. in sand, 0.0; at 12 in. in sand, 0.0 cc.; at top of wave line, 1 in. deep in sand, 0.82; 1.5 in. in sand, 3.6; 3 in. in sand 0.67; 5 in. in sand, 0.19 cc.; 6 in. above wave line, 7 in. deep in sand, 1.2 cc. On the beaches of Bird and Sheepshead Shoals more extensive observations were made under various tidal conditions. The results are shown in Table 3. When a tide is falling oxygen percolates into the surfaces of beaches somewhat, but usually there is little or none below 2-3 inches.

TABLE 3. Average amount of oxygen in and above sand beaches on Bird and Sheepshead Shoals, Beaufort, N. C., in cubic centimeters per liter.

Source of sample	Surface water	In sand; depth in inches							
		0	1	2	3	4	5	6	7
cc. of O_2.........	4.67	1.90	1.01	0.28	0.29	0.20	0.35	0.0	0.0
No. of samples....	3	4	6	3	6	3	1	1	1
No. without O_2...	0	0	0	1	4	1	0	1	1

Ionization.—On the beach along the open sea and offshore above bottom at a depth of 5.5 m. near Fort Macon during the summer of 1939 pH was 8.6; at a depth of 5.5 m., 8.6; and in the sand in an Ocypode hole, 8.7. In the water along the channel inside Fort Macon pH at the surface was 8.5, 8.6, and 8.8; at depths of 5.5 and 6.5, 8.6 and 8.5; at water's edge 3 in. deep in sand, 7.9. On Bird and Sheepshead Shoals 6 surface samples had a pH average of 8.0; two at a depth of 1 m., 8.3; in sand as indicated at following depths: 4 at 1 in., 7.9; 3 at 2 in., 7.9; 5 at 3 in., 7.8; 1 at 4 in., 8.0; 1 at 5 in., 8.0. As oxygen decreases, carbon dioxide doubtless increases and this will explain, at least in part, the swing toward acidity at increasing depths in sand.

FAUNA OF BEAUFORT SAND BEACHES

Data from a particular source are limited because any collecting method is selective. For example blue crabs *(Callinectes sapidus)* are seldom caught in a dredge, but if a trawl is dragged over the same bottom many blue crabs may be captured. These crabs can swim fast enough to avoid the small aperture of a dredge, but a trawl spreads too widely for them to escape. This section will be devoted to the animals collected by various methods on and in the sand beaches at Beaufort.

Animals Collected in Salve Boxes

In 1939 salve boxes after they had been filled in the field were "extracted" by shaking with water and filtering off the animals thus washed out. Twenty-eight types of microscopic animals were found. Those that occurred in greatest numbers are shown in Table 4.

The figures show that nematodes, copepods, polychaetes, ostracods, Haustorius, nauplei, and young clams occurred in greatest numbers in the sands of Bird and Sheepshead Shoals, where there was most humus and which were completely covered by every high tide. Asterigerina, Donax, acoel and rhabdocoel flatworms were most abundant in the wave-swept but gently sloping beaches along the open sea outside Fort Macon (Stations IV, V). Among the animals collected on all three beaches none showed greatest numbers on the lee-shore, abruptly sloping beaches inside Fort Macon near the ship channel (Fig. 1; Stations I-III).

Various protozoans occurred on all beaches. Ciliates were very prevalent in many salve boxes from outside Fort Macon (Stations IV, V). Oligochaetes were present in small numbers at all stations. Mysidaceans were taken once at each of Stations II and VI, but not along the open sea. Mites were collected once at each of Stations IV and V. Emerita, Stauronereis, Pontharpina and an ant were found only once, in each case outside Fort Macon (IV, V). Annelid larvae, crab zoeae, and a stauromedusan were found once on the beach inside Fort Macon (I, II, III). From the beaches on Bird and Sheepshead Shoals, and not at other stations, the following were taken: Cyclaspis, Nassarius, Terebra, Sphaeroma, chironomid larva, and a dolichopodid (?) larva.

During the summer of 1941 a few salve box samples were not washed but examined directly by teasing small quantities of sand in a thin film of sea water across a glass plate under a binocular microscope. Four collections from Fort Macon beach, outside (Stations IV, V) from mid- and low-tide levels gave the following averages per box: Asterigerina, 114.3; Archiloa, 5.8; Quinqueloculina, 4.3; nematodes, 3.3; ostracods, 0.8; copepods, 0.5; Donax, 0.3. Five boxes from Bird and Sheepshead Shoals (VI, VII) from high tide (1), mid-tide (2), and low tide (2) levels showed the following averages: Asterigerina, 207.6; nematodes, 62.4; Quinqueloculina, 13.4; annelids, 11.4; Archiloa, 10.6; copepods, 5.6; Haustorius, 2.8;

ostracods, 2.6; Donax, 1.4. These observations are limited, but in general they support those made in

TABLE 4. Numbers of more common microscopic animals collected in duplicate salve box samples in the summer of 1939 from sand beaches. Figures indicate number of times present and average per box; +, less than 0.1.

	No. of Samples	Nematodes	Copepods	Asterigerina	Polychaetes	Ostracods	Haustorius	Donax	Acoels	Rhabdocoels	Nauplei	Clams
Ft. Macon, Outside	86											
High Tide Mark	10	8 2.0	3 0.5	2 0.2	1 0.1			2 0.2			0.1	
'Tween Tides	22	21 3.1	9 1.8	6 1.1	1 +	1 +	1 +	0.1	0.2			
Low Tide Mark	24	19 2.7	9 2.3	12 0.8	2 0.1			6 0.5	0.1			4 0.3
0.5 m. below L.T.M.	18	14 2.4		17 3.6	3 0.2	1 +	4 0.2			2 0.1	2 0.1	1 0.2
3.5 m. deep	1	1 10.0	1 16.0	1 1.0		1 3.0						
3.5–6.5 m. deep	3	3 7.0	1 0.3	1 0.3	1 0.3		1 0.3			1 2.0		
Tide Pool	8	8 4.1	3 1.0	8 3.3			2 0.2					3 2.0
Average		10.6 4.5	3.7 3.1	6.7 1.3	1.1 0.1	0.1 0.1	1.1 0.1	1.4 0.1	0.9 +	0.4 0.3	0.4 +	1.0 0.4
Ft. Macon, Inside	78											
High Tide Mark	6	2 0.7		1 1.5								
'Tween Tides	24	17 1.6	5 1.4	4 0.2		1 +	2 0.1	1 +	1 +	1 +	1 0.2	
Low Tide Mark	18	13 2.6	2 0.1	4 0.5				2 0.2				1 0.1
0.5 m. below L.T.M.	12	9 4.0	1 0.2	7 2.4	1 0.1	1 0.7						2 0.3
0–3 m. deep	2	2 11.0	15.5	1 1.0	1 +							
4.5 m. deep	2	2 27.0	2 5.0			1 3.0						
Sand, 3 cm. deep	12	1 1.5	1 0.1	1 0.3								1 0.1
Sand, 12 cm. deep	2	1 1.0		1 1.0								
Average		6.7 6.2	1.5 2.5	2.4 0.9	0.3 +	0.3 0.5	0.1 +	0.3 +	0.4 +	0.1 +	0.1 +	0.6 0.1
Bird & Sheepshead Shoals	126											
High Tide Mark	13	13 14.0	12 11.3	2 0.2	4 0.8	9 3.5			1 0.1	5 1.0	2 0.4	2 0.2
'Tween Tides	25	24 12.2	19 17.2	6 1.0	4 1.2	18 4.0	5 0.3		1 0.1	2 0.3	1 0.1	4 0.4
Low Tide Mark	24	24 10.0	15 19.9	6 +	8 0.7	8 0.6		2 0.1	1 +	2 0.1	1 +	5 0.2
0.5 m. below L.T.M.	16	16 12.1	15 25.0	14 1.0	4 0.3	3 0.2	5 0.4		1 0.2	2 0.3		
Tide Pool	10	10 9.0	10 9.8	4 1.4	1 0.1	8 5.7				1 0.1	2 0.1	4 0.6
2 m. deep	2	2 1.5	1 1.0	1 1.0			1 0.5					1 0.5
Sand, 8 cm. deep	21	19 4.2	11 1.6	9 0.5	1 +	4 0.2				1 +		1 +
Sand, 15 cm. deep	15	15 3.3	5 1.8	6 0.7	1 0.8	1 0.1	1 0.1	1 0.1		1 +		
Average		15.4 8.3	11.0 11.0	0.6 0.7	2.9 0.5	6.4 1.8	0.9 0.2	0.4 +	0.5 +	1.8 0.2	0.6 0.1	2.1 0.2

1939. There are apparently more nematodes, copepods, and ostracods on inundated beaches of Bird and Sheepshead Shoals than on the dune-bordered beaches on the open sea.

As the capacity of a salve box was 17.5 cc., rough estimates may be made from Table 3 of the average number of animals per liter in the surface sands of Beaufort beaches as follows:

Fort Macon, outside (IV, V): nematodes, 260; copepods, 180; Asterigerina, 75; etc.

Fort Macon, inside (I, II, III): nematodes, 350; copepods, 140; Asterigerina, 50; etc.

Bird and Sheepshead Shoals (VI, VII): nematodes, 480; copepods, 630; Asterigerina, 40; ostracods, 100; etc.

In routine examinations it is difficult to tell whether such animals as the foraminiferan, Asterigerina, or minute snails and clams are alive or merely empty shells. The value of our counts on such animals is therefore more or less doubtful.

Such figures as those just given are not very significant, for the collecting methods used warp results. The few observations in 1941 show that many more Asterigerinas are probably present than the washing method used in 1939 indicated, but show fewer copepods and nematodes. However, Table 4 and the accompanying discussion do give information that shows in a general way what the microfauna in Beaufort sand beaches is. There is often great irregularity in distribution. Beach animals such as Emerita and Donax are often abundant in one place and absent in another. Microcospic animals collect where there are bird feces or other organic remains.

ANIMALS COLLECTED BY SIFTING SAND

Thirty-two types of animals were captured by sifting beach sands through coarse and fine sieves. These of course were of larger size than those taken in salve boxes. Table 5 shows the distribution of some of the more common animals. Of the four commonest

TABLE 5. Animals sifted from beach sands, 1941. Capacity of sieves 6.5 liters; mesh, 6 per centimeter. Figures indicate average per sieve.

	Ft. Macon, Outside					Ft. Macon, Inside				Bird and Sheepshead Shoals				
	H.T.M.	½ T.	L.T.M.	0.5 m. below L.T.M.	3.5 m. deep	H.T.M.	½ T.	L.T.M.	0.5 m. below L.T.M.	H.T.M.	½ T.	L.T.M.	0.5 m. below L.T.M.	3.5 m. deep
No. of samples	16	14	16	10	24	12	14	10	10	14	14	16	12	36
Haustorius	0.7	2.2	1.7	6.5	3.3	1.2	2.1		4.7	2.3	112.0	136.0	46.0	9.6	3.1
Emerita	0	1.5	+	0.2	0	0	0	3.4	0	0	0	0	0	0.1
Donax	0.3	13.5	11.0	0.3	1.3	0.1	52.3	160.0	0.2	3.9	0.7	0.3	0.0	+
Annelids	0	0.1	0.7	0	2.3	0	0.2	0.7	0.7	31.1	6.0	1.8	2.2	?
Chiridotea	0.1	0.2	+	0.1	0	0	0.4	0	0	+	0	0	0	0
Terebra	0	0	0	0	0	0	0	0	0	0	0.2	0.4	0.6	0

types there shown, Haustorius and annelids were most abundant on Bird and Sheepshead Shoals (Fig. 1), less common on the narrow, abruptly sloping beaches inside Fort Macon, and uncommon along the open sea. Emerita was the opposite; abundant along the open sea, less inside Fort Macon, and rare on the shoals. Donax occurred in maximum numbers inside Fort Macon, was common on the open ocean, and infrequent on the shoals studied.

Of course the fact that a particular animal was not taken in a sieve at a particular place did not necessarily mean that it did not live there. Sieving is only one means of judging frequency of distributions. Nine animals were taken only on the two shoals studied—Terebra, Branchiostoma (3-4 m.), Leptosynapta, Cyathura, Balanoglossus (3 m.), Nassarius vibex, fly larvae, Spissula, and Lysiosquilla. Sipunculids and tiger beetle larvae were found only inside Fort Macon (Stations I-III). Michtheimysis was taken only on the beach outside Fort Macon (IV, V), and Orchestia was found only there and on Shackleford Bank. On Bird and Sheepshead Shoals and outside Fort Macon several types were taken— Pagurus longicarpus (usually just below low tide mark, or deeper), Dissodactylus on sand dollars (Mellita), Mellita, Pontharpina (also on Shackleford Bank) and always in deeper water (3-5 m.), Ogyris below low tide mark, young clams, and Olivella (2 spp.); Chiridotea was not common anywhere but was found on both sides of Fort Macon. Nemerteans occurred on the shoals and inside Fort Macon. Talorchestia and small specimens of Venus and Clibanarius were sifted from the beaches of Shark Shoal (Fig. 1). Tellina occurred in moderate depths off Bird Shoal and inside Shackleford Bank.

Such types as Emerita and Lepidopa are most often found where waves from the open ocean beat across gradually sloping sand beaches. Donax also flourishes among beating waves but is most frequent where there is an abrupt slope. Annelids and Haustorius reach maximum numbers where flat beaches are completely covered by high tides.

Only the results of siftings for certain types in fine sieves during the summer of 1941 are presented in Table 5, but 85 routine sieve catches in 1939 agree in general with the data given. The results for coarse sieves (1939, 107; 1941, 62) show fewer animals but indicate similar distribution of populations. The findings for sieve catches will be considered again under zonation.

Animals Collected by Digging

By digging on a few occasions where the beach showed a burrow or other signs of disturbance without sifting or other means of capture the animals in the following list were turned out of sand the number of times indicated during 1941.

Fort Macon Beach, outside: Emerita 3, Lysiosquilla 3, Donax 2, Haustorius 2, Callichirus 2, Arenaeus 2, Busycon carica 2, Ogyris 2, Olivella 2, Michtheimysis 2, nemertean 1, annelid 1, Chiridotea, 1, Lepidopa 1, Libinia 1, Persephonia 1, Thyone 4.

Bird and Sheepshead Shoals: Spissula 9, Arenicola 7, Balanoglossus 7, Venus 7, Terebra 6, unidentified annelids 5, sipunculids 5, Polynices 5, Sinum 5, Callianassa 5, Moira 4, Chaetopterus 4, Glycera 3, Leptosynapta 3, Mellita 3, Busycon canaliculala 3, Pinnixia cristata 3, Macrocallista 3, Pecten 2, Dosinia 2, Tagelus 2, Divaricella 2, Oliva 2, Olivella 2, nemerteans 2, Albunea 2, Lysiosquilla 2, Pagurus longicarpus 2, Phascolosoma 1, Aricia 1, Nephthes 1, Scoloptos 1, Clymanella 1, Petaloproctus 1, Arenicola eggs 1, Thallassema 1, Echiuris 1, Cerebratulus 1, Busycon carica 1, Polynices eggs 1, Ensis 1, Nassarius obsoleta 1, Donax 1, Polyoyx 1, Persephonia 1, Euceramus 1, amphipod 1, Emerita 1, Limulus 1, Ophiopholis 1.

It is difficult to make digging an impersonal method of collecting. In spite of himself, a man tends to dig where he will get something. Though the numbers presented by no means represent mathematical differences between beaches on the open ocean and those on shoals in sounds, they have some significance in showing essential characteristics of the two faunas. Lepidopa, Emerita, Aranaeus, Donax, Ogyris, Lepidopa, and Chiridotea are characteristic of sand beaches on the open ocean. On the tide-covered sand flats in sounds many clams, annelids, heart urchins, king crabs, and crustaceans are present which do not occur along the open sea.

Animals Collected by Seining

Seine hauls with a 30-ft. minnow seine yielded quite a variety of fishes and some other animals. The results of 19 hauls during the summer of 1939 and 49 during that of 1941 are shown in Table 6. The silversides and killifish are apparently the most abundant small fishes over sandy beaches about Beaufort Harbor.

Only species that were taken in two or three localities are shown in the table. Those that occurred over only one beach during both summers were as follows:

Fort Macon, outside: Callinectes ornatus 4-0.7; Orchestia grillus 1-0.1; colonial ascidian 2-0.2; Caprella linearis 2-0.2; Neopanope texana 4-0.4; squid eggs 1-0.4; Thyone briareus 2-0.2; Microciona prolifera 1-0.2; Libinia dubia 1-0.1; Erychthys stomatopod larvae 3-2.9; Filefish, Stephanolepis hispidus, 1-0.1; Tethys protea 1-0.1.

Fort Macon, inside: Pagurus pollicaris, 2-0.3; barracuda, Sphyraena borealis, 1-0.1; Arbacia punctulata, 1-0.3; sea robins: Prionotus carolinus 1-0.3, P. scitulus 1-0.3; medusae 1-1-3.

Bird and Sheepshead Shoals: Mellita quinquiesperforata 1-0.2; Crago septemspinosus 3-0.3; Olivella mutica 3-1.8; Nassarius trivittata 2-2.7; N. vibex 2-0.1; N. obsoleta 1-1.3; Portunus gibbesii 2-0.8; pajaarito, Hyporhamphus hildebrandi 1-0.1.

Some small animals, such as various swimming amphipods and the sessile Caprella, are often brought in with floating algae and appear in seine hauls or in seaweeds cast up on the beach.

Some animals (lizard fish, Terebra, etc.) are seldom

TABLE 6. Results of 68 seine hauls on sand beaches during two summers. Numbers are average catches.

Place	Ft. Macon, Outside				Ft. Macon, Inside				Bird and Sheepshead Shoals			
No. of hauls	10		16		3		18		6		15	
Summer	1939		1941		1939		1941		1939		1941	
Frequency	No. Times	Ave. No.	No. Times	Ave. No.	No. Times	Ave. No.	No. Times	Ave. No.	No. Times	Ave. No.	No. Times	Ave. No.
Silverside *Menidia menidia*	10	112.7	12	18.1	2	56.0	8	4.9	6	24.5	10	116.8
Anchovy *Anchoviella mitchilli*	7	31.7	1	0.3	1	50.2					2	0.3
Killifish *Fundulus majalis*	1	0.5	5	4.3	1	1.3	5	2.1	3	13.5	6	41.2
Pompano *Trachinotus carolinus*	8	11.4	4	2.3			2	0.3				
Pinfish *Lagodon rhomboides*	2	0.2			1	0.7	3	3.2			2	0.3
Lizard Fish *Snyodus faetens*					3	2.7	1	0.1	1	0.2	1	0.1
Blue Crab *Callinectes sapidus*	2	0.3	7	3.4			6	2.0	3	0.7	11	2.5
Northern Kingfish *Menticirrhus saxatilis*	6	4.2	5	1.4	1	0.3			1	0.2	1	0.1
Flounder *Paralichthys dentatus*	2	0.2	2	0.2			4	0.5	2	0.5	5	0.3
Flounder *Paralichthys albiguttulus*					2	0.7						
Portunid Crab *Aranaeus cribrarius*	5	0.5	10	5.1					1	0.2	1	0.1
Croaker *Micropogon undulatus*			6	1.4			4	3.4				
Mole "Crab" *Emerita talpoida*	1	0.7	3	1.1	1	0.3	6	1.0				
Hermit Crab *Pagurus longicarpus*			3	0.3			2	0.2	1	0.5	6	2.4
Jack *Caranx hippos*			3	0.5							1	0.5
Mullet *Mugil cephalus*			1	0.2			6	4.0				
Spot *Leiostomus xanthurus*			2	1.0			4	1.8			1	0.1
Pipefish *Syngnathus fuscus*			2	0.2			2	0.1				
Lady Crab *Ovalipes ocellatus*			2	0.3			3	0.4				
Triggerfish *Balistes carolinensis*			2	0.1			3	0.4				
Snail *Terebra dislocata*							1	0.1	1	0.2		
Beach Clam *Donax variabilis*			3	0.9					1	0.2		
Ascidian *Styela partita*					1	0.3			1	0.2		
Ctenophore *Mnemiopsis leidyi*	1	0.1							4	18.3		

or never seined on beaches along the open sea. Others (Emerita, etc.) occur more often there, and are rare or absent on shoals in sounds.

CATCHES WITH RAKE NET

Rake net (Fig. 2) catches were suited to capture crabs and other animals of suitable size that frequent the surfaces of sandy shores below water line.

In Table 7 only the species that occurred on at least two beaches are included. Other animals that were raked up on only one beach were as follows:

Fort Macon, outside: Kingfish, *Menticirrhus saxtilis* 1; anchovy, *Anchiobiella mitchilli* 1; spider crab, *Libinia dubia* 1; nudibranch, *Scyllaea pelagica* 4; shrimp, *Latreutes enciferus* 1; snail, *Oliva sayana* 1; holothurian, *Thyone briareus* 3.

TABLE 7. Rake net catches on sand beaches, during the summer of 1941.

Locality	Ft. Macon, Outside		Ft. Macon, Inside		Bird and Sheepshead Shoals	
No. of hauls	21		20		21	
	No. times	Ave.	No. times	Ave.	No. times	Ave.
Portunid Crab *Arenaeus cribrarius*	7	2.4	1	0.1	..	...
Sand Dollar *Mellita quinquiesperforata*	...	...	..	...	10	8.2
Blue Crab *Callinectes sapidus*	3	0.5	3	0.3	3	0.2
Lady Crab *Ovalipes ocellatus*	2	0.1	3	0.2	2	0.1
Mole Crab *Emerita talpoida*	1	0.1	2	0.1	..	...
Portunid Crab *Callinectes ornatus*	1	0.1	..	...	1	0.1
Hermit Crab *Pagurus longicarpus*	3	0.3	..	...	12	2.3
Flounder *Paralichthys dentatus*	..	...	2	0.1	4	0.3

Fort Macon, inside: Beach clams, *Donax variabilis* 3; *Spissula solidissima* 1; starfish, *Luidia* sp. 1; triggerfish, *Balistes carolinensis* 2; jack, *Caranx hippos* 1.

Bird and Sheepshead Shoals: Hermit crab, *Pagurus pollicaris* 2; snails, *Polynices heros* 1; *Nassarius vibex* 8-0.9; *Terebra dislocata* 10-2.1; *Olivella mutica* 1; *Crepidula fornicata* 1; shrimp, *Crago septemspinosus* 1; *Arenicola* egg string 1; compound ascidian 1; sand dollar crab, *Dissodactylus mellitae* 2-0.2; kingfish, *Menticirrhus saxatilis* 1.

Table 7 indicates clearly that Arenaeus prefers wave-swept open-sea beaches and that Mellita is most abundant on bars in sounds. Some crabs, such as Ovalipes and Callinectes, appear to wander over all sorts of sand beaches.

ANIMALS CAUGHT BY DREDGING

Table 8 shows the frequency of animals caught in dredge hauls along two or three different types of beaches. Some were distributed everywhere a little way offshore (Styela, Ovalipes, Mellita), others were more abundant toward the open sea (*Pagurus pollicaris*, Aranaeus, *Olivella floralia*, Asterias, Renilla), some occurred in greatest numbers on shoals in sounds (*Pagurus longicarpus*, Spissula, Terebra, Nassarius, Sinum), and some were most often dredged along banks on the side away from the sea (Neopanope, Anachis, *Olivella mutica*, Crepidula, Pontharpina).

Animals that were dredged on only one beach showed distributions as follows:

Fort Macon, outside: A medusa (Chiroplasmus?) 2-0.5; Adamsia on hermit crab shells 2-0.2; *Busycon carica* 2-0.3; *Donax variabilis* 3-0.5; a colonial ascidian 1-0.2; *Ascidia* sp. 1-0.1; *Nototropis minakoi* 2-2.2; *Petaloproctus socialis* 4-3.1; lizard fish, *Synodus faetens* 1-0.1; triggerfish, *Balistes carolinensis* 1-0.1; porcupine fish, *Diodon hystrix* 1-0.3; shrimp, *Parapenaeus politus* 1-0.2; *Pontharpina epistoma* 1-0.2.

TABLE 8. Animals caught in dredge hauls in depths of 3-5 meters, 1941.

	Ft. Macon, Outside		Inside Ft. Macon and Shakleford Bank		Bird and Sheepshead Shoals	
No. of hauls	12		13		11	
	No. times	Ave.	No. times	Ave.	No. times	Ave.
Mellita						
quinquiesperforata	12	23.1	6	5.0	10	31.5
Asterias vulgaris	1	0.1	7	1.1	..	....
Unidentified *annelids*	1	0.3	7	4.0	..	....
Pagurus long'carpus	12	26.5	13	36.0	11	85.1
Pagurus pollicaris	5	3.6	3	0.8	1	0.1
Libinia dubia	1	0.1	1	0.1	..	....
Dissodactylus mellitae	1	0.3	5	1.2	1	0.1
Emerita talpoida	2	0.6	..	....	2	0.4
Neopanope texana	..	....	6	1.7	1	0.1
Ovalipes oculatus	5	0.4	1	0.1	4	0.4
Arenaeus cribrarius	6	0.9	4	0.6	..	....
Spissula solidissima	4	0.4	2	0.2	5	1.1
Arca sp.	1	0.3	4	0.4	..	....
Anachis avara	2	0.5	4	6.2	..	....
Olivella mutica	9	3.8	12	13.1	5	1.7
Olivella floralia	1	0.3	?	?	..	....
Crepidula fornicata	1	0.3	3	0.8	..	....
Terebra dislocata	..	....	5	1.5	5	3.2
Nassarius vibex	..	....	4	2.5	1	1.4
Sinum directivum	..	....	1	0.1	1	0.1
Michtheimysis	1	0.1	4	1.3	..	....
Styela partita	2	0.2	3	0.3	1	0.2
Renilla reniformis	2	0.4	1	0.1	..	....
Pontharpina floridana	..	....	8	2.6	1	0.1
Prionotus carolinus	1	0.1	3	0.2	4	0.5
Paralichthys dentatus	1	0.1	..	....	1	0.1

Fort Macon, inside: *Schizoporella unicornis* 2-0.1; *Hydroides hexagonus* 3-0.2; *Nereis limbata* 1-0.1; *Leptogorgia vingulata* 4-5.4; *Arbacia punctulata* 3-0.4; *Tellina* sp. 5-1.1; *Chaetopleura* sp. 3-0.9; *Urosalpinx cinereus* 5-2.2; *Peneus setiferus* 1-0.2; *Hippolysmata wurdmanni* 1-0.1; *Glycera* sp. 1-0.1; *Clymenella torquata* 2-0.2; *Clione cancellata* 1-0.1; ophiuroid 2-0.2; *Bankia gouldi* 2-0.2; *Heterocrypta granulata* 4-0.4; *Branchiostoma virginiae* 3-0.3; *Haustorius* sp. 2-0.2; *Turbonilla dalli* 1-0.1; *Lithophaga bisulcata* 4-0.3; *Thallasema mellita* 4-0.5; *Euceramus praelongus* 2-0.5; *Ogyris alphaerostris* 1-0.1; *Cardium robustum* 1-0.2; *Cucumaria pulcherrima* 1-0.1; Spondylus? 2-0.3; *Lysianopsis alba* 2-0.2; *Lembos smithi* 1-0.2; *Melita fresnilii* 1-0.2; *Unciola irrorata* 2-0.8; *Erichthonius* sp. 1-0.1; *Leucothoe spinicarpa* 1-0.1.

Bird and Sheepshead Shoals: *Portunus spinimanus*

2-0.3; *Ostrea cristata* 1-0.1; *Microciona prolifera* 1-0.1.

It is apparent that a greater variety of animals were dredged on sand beaches along the sides of Bogue and Shackleford Banks (Fig. 1) than along the beaches on the open sea or near those along shoals in sounds.

ANIMALS CAUGHT BY TRAWLING

During the summers of 1939 and 1941 five hauls each year, with a 30-ft. otter trawl were made offshore along Bogue Bank beyond Stations IV and V (Fig. 1). These were about a mile in length.

Three hauls at a depth of about three meters caught the following animals the number of times indicated and in about the total numbers given: Arenaeus 2-7; Ovalipes 1-5; *Callinectes sapidus* 1-20; *Peneus setiferus* 1-30; *Pagurus pollicaris* 3-29; *P. longicarpus* 1-15; Chloridella 1-5; Loligo 1-8; Astropecten 1-1; Mellita 2-9; Thyone 1-1; Adamsia 2-14; Mnemiopsis 1-1; croaker, *Micropogon undulatus* 1-20; Filefish, *Stephanolepsis hispidus* 1-1; Northern kingfish, *Menticirrhus saxtilis* 1-1; butterfly ray, *Pteroplatea micrura* 1-12; sea robin, *Prionotus* sp. 2-12.

Three hauls at 7 m. yielded: Ovalipes 1-5; Persephonia 1-3; Dissodaclytus 1-4; *Peneus setiferus* 2-25; *Pagurus pollicaris* 3-23; Chloridella 1-1; Loligo 2-6; Astropecten 1-2; Mellita 2-301; Moira 1-1; Mnemiopsis 1-1; Gorgonia 1-1; *Busycon* sp. 1-2; Terebra 1-20; *Olivella* sp. 1-10; Adamsia 1-15; croaker 1-1; cutlass fish, *Trichiurus lepturus*, 1-1; threadfish, *Alectis ciliaris* 1-1; flounder, *Paralychthys dentatus* 1-2; sand shark, *Carcharias littoralis* 1-1; sting ray, *Dasyatis americana* 2-1; sea robin, *Prionotus* sp., 2-14.

At a depth of 15 m. three trawls showed: *Libinia dubia* 1-10; Hepatus 1-25; Ovalipes 1-15; Persephonia 1-3; *Callinectes sapidus* 2-30; *Peneus setiferus* 1-100; *Pagurus pollicaris* 2-11; Chloridella 1-15; medusa 1-1; Astrangia 1-10; Thyone 1-2; *Asterias forbesi* 2-7; Astropecten 1-1; Luidia 1-2; *Polynices heros* 1-1; Polynices egg collar 2-2; *Busycon* sp. 1-1; Eupleura 1-1; Loligo 5-9; Renilla 1-1; croaker 2-200; pinfish, *Lagodon rhomboides*, 2-150; cutlass fish, *Trichiurus lepturus* 1-25; silversides, *Menidia menidia* 1-10; butterfish, *Prionotus tricanthus* 1-10; lizard fish, *Snyodus faetens* 1-25; sea bass, *Centropristus striatus* 1-25; sea trout, *Cynoscion regalis* 1-20; hogfish, *Lachnolaimus maximus* 1-25; sea robin, *Prionotus* sp. 2-26; tonguefish, *Symphurus plaguisa* 1-2; flounder, *Paralichthys dentatus*, 2-19.

Some animals were found at all depths where trawls were made (Peneus, *Pagurus pollicaris*, Chloridella, squids, sea robins). Some were found only in shallower waters (Arenaeus, *Pagurus longicarpus*, butterfly ray, kingfish, and filefish); others occurred only at intermediate depths (Gorgonia, Renilla, Moira, Luidia, Olivella, Terebra, Busycon, sand shark, sting ray, threadfish); others only in deeper waters (Astrangia, medusa, Hepatus, Libinia, Polynices, pinfish, silversides, butterfish, lizard fish, sea bass, sea trout, tonguefish, hogfish). From other sources it

is known that such evidences of localized distribution are not in most cases significant; the number of observations is too small. However, the trawls all together indicate what types of larger animals occur over sandy bottoms alongshore at moderate depths.

ANIMALS OBSERVED WHEN WALKING ALONG BEACHES

During the summer of 1941 records were kept of animals seen on sands above low tide mark at ebb tide. It is of interest that only one of the animals thus observed on the beach along the open sea (Physalia) was the same as any of those recorded from Bird and Sheepshead Shoals. The number of times an animal was seen and the total number observed at the two localities was as follows:

Fort Macon Beach, outside: Physalia 1-1; Emerita 2-2; Neopanope 1-1; Ocypode 5-8; Metaphorhapis 1-1; Latreutes 1-1; Ligyda 1-1; Mychtheimysis 2-2; compound ascidian 1-1; triggerfish 1-1; pipefish 1-1. Some of these were associated with seaweeds that had washed ashore.

Bird and Sheepshead Shoals: Physalia 1-3; Mellita 3-3; Moira 1-1; Balanoglossus 1-1; Arenicola eggs 2-2; Cardium 1-1; Spissula 1-1; Pecten 1-1; Venus 1-1; Sinum 3-3; Terebra 2-11; *Nassarius vibex* 1-3; *Olivella floralia* 3-4; *Busycon carica* 4-4; Busycon egg case 1-1; Polynices egg collars 3-3; Oliva 1-1; *Callinectes sapidus* 4-19; Persephonia 1-1; Peneus 2-2; Clibinarius 2-2; *Pagurus pollicaris* 1-1; *P. longicarpus* 2-28; Albunea 2-2; Lepidopa 1-1; Callianassa 1-1; Lysiosquilla 1-1; Chiridotea 1-1; Limulus 4-4; Fundulus 1-1.

Even superficial examination shows very apparent differences between the faunas of beaches along the open sea and those on shoals in sounds.

ZONATION ON SAND BEACHES

Animals that live high on sand beaches are exposed more or less to desiccation and wide variations in temperatures but are in less danger of capture by predators that come up with each rising tide. Killifish, silversides, blue crabs, and other predators commonly follow each tide inshore and devour anything they can find. Beach animals are "between the devil and the deep sea." They are bedeviled when the tide is out by long-billed shore birds that probe the sand to turn them out, rooting hogs, raccoons, and other enemies. Not only do they live in an oxygen-poor, shifting substratum which is often overturned and completely rearranged by wind-driven tides and rolling waves, but they are continually beset by enemies that come from land or sea.

Some animals have left the sea altogether. The ghost crab (Ocypode) lives in deep burrows and comes out at night to hunt along the edge of the ocean for organic remains that may serve as food. Its burrows may be found among dunes at considerable distances from water. It is able to respire in air for some time, but often plunges into the ocean to wet its gills and branchial chambers. Certain amphipods (Orchestia, Talorchestia) live in sand

along drift lines; they are killed when submerged in fresh water and avoid sea water, but never wander far from ocean beaches. The drift line with its accumulations of organic rubbish serves as a home for many scavengers and predators that have come from land. These include beetles, flies, earwigs, collembolans, spiders, etc.

Our catches with salve box (Table 4), sieve (5), rake net, diving hood, dredge, and trawl give a general idea of the zonal distribution of animals on sand beaches at Beaufort. Only a few types are considered.

Nematodes.—Salve box samples from the surface of beaches during 1939 (Table 4) showed most nematodes below low tide mark along the open ocean and the Fort Macon beach inside. On shoals in sounds they were more abundant and rather equally distributed at all higher levels, but were fewer below low tide mark. At various depths in sand there was a slight decrease in their numbers up to 12-15 cm.

Copepods.—Copepods were more abundant just below low tide mark on all types of sand beaches studied and decreased rapidly below the surface of sand.

Ostracods.—In salve box samples from beaches near the open sea (Stations I-V) ostracods were most common below low tide mark but on inundated shoals (VI, VII) they were not common below low tide mark and occurred in considerable numbers at high levels and in tide pools. All ostracods collected were littoral species. They "in all probability do not belong to the regular fauna which exists among sand grains . . . they are too large . . . . The family Cytheridae, to which all belong, is composed of strictly bottom-dwelling forms which possess no power of swimming" (Tressler 1940).

Haustorius.—Data from sieve catches (Table 5) show that this burrowing amphipod was most abundant between tides and occurred in much greater numbers on inundated shoals than on open sea beaches. It was more common at high tide than low. On the beach inside Fort Macon, however, it was most numerous at low tide mark.

Emerita.—This burrowing crustacean moves up and down with tides somewhat but sieve catches for 1939 show it to be nearly absent at high tide mark, abundant in the intertidal region, few at low tide mark, and very rare in low-lying pools and below low tide mark.

Donax.—This little burrowing clam, like Emerita, moves back and forth over beaches with tides. Sieve catches for 1939 and 1941 show many in the intertidal region and some at low tide mark, but very few above and below those levels. This clam is typically intertidal and lives where waves roll, but may at times be found elsewhere. It occurred in greatest numbers on the abruptly sloping beaches east of Fort Macon.

Polychaetes.—These annelids on the beaches around Fort Macon were most common near low tide mark, but on the inundated shoals in sounds were most numerous at the highest levels.

Terebra.—This snail was rare except on inundated shoals, where it was most numerous just below low tide mark.

Chiridotea.—This isopod was absent from shoals and on ocean beaches was most common in the intertidal zone.

Mellita.—On beaches sand dollars were found to be most numerous at and immediately below low tide mark. Dredge and trawl hauls indicate that they are in some places abundant in deeper waters.

Lepidopa.—This burrowing crustacean was usually found in small numbers at or immediately below low tide mark.

Arenaeus.—This active portunid crab was often caught in rake net hauls among waves at low tide mark. Where waves roll it may often be seen to scurry across the sand and burrow backwards to cover all but eyes, antennae, and front.

Ogyris.—This little shrimp-like burrower with long eyestalks was usually found on firm bars of fine sand just offshore (1 m. deep) along the open ocean.

Branchiostoma.—This cephalochordate was caught only in sand brought up from depths of 3-5 meters near Bird and Sheepshead Shoals or inside Shackleford Bank. At times other observers have taken specimens in shallow water but we never found any.

Hermit Crabs.—There are three common hermit crabs at Beaufort. *Pagurus longicarpus* is usually found in shallow waters, especially along the borders of shoals in sounds; *Clibanarius vittatus* is found in similar situations but usually in quieter waters, as along the shores of mud flats; *Pagurus pollicaris* is found most often in the open ocean and ranges to considerable depths.

Callianassa.—This crustacean lives in deep (1 m.) burrows on flat beaches that are inundated at high tide and exposed at low tide. It is common on Bird and Sheepshead Shoals and occurs in suitable places on the beaches along the open sea outside Fort Macon.

Lysiosquilla.—This stomatopod has similar distribution and burrowing habits to Calianassa.

Perhaps enough examples have been given from data previously presented (Tables 4-8, etc.) to give a general idea of zonal arrangements on Beaufort sand beaches.

Above the drift line, and spreading at times even down into the intertidal level, lives the ghost crab. Along the drift line are many small scavengers and predators, mostly with terrestrial affinities, but also including some marine types. No animals are characteristic of high tide level as such. On flat, inundated beaches in the intertidal zone Haustorius, Callianassa, and polychaetes are typical. On steeper beaches subject to greater wave actions Emerita and Donax flourish. At low tide mark on such beaches Lepidopa is to be found. Immediately below low tide mark Mellita, Terebra, Ogyris, *Pagurus longicarpus*, Thyone, Cardium, and Oliva are most common. Nematodes, copepods, and ostracods occur at all levels but usually become most numerous below low tide mark. Polychaetes are abundant on the tops

of inundated flats on shoals and decrease below low tide mark, but show the opposite distribution on wave-swept, dune-bordered beaches. In deep waters offshore Renilla, blue crabs, squids, sand dollars, sea robins, and flounders may be mentioned as characteristic animals. Some of these have ranges that extend to the intertidal zone, others are restricted to deep waters.

ADAPTATIONS OF SAND BEACH ANIMALS

Animals that live in shifting sands on marine beaches are often peculiarly adapted to the unusual conditions of life in which they exist. They are adapted in their ranges of toleration to environmental factors, and for feeding, burrowing, breathing, reproducing, etc.

Tolerations.—Psammobionts live in a changeful environment. The ebb and flow of tides twice a day alternately flood their habitat and then leave it more or less exposed to desiccation by winds. When a tide covers a beach, oxygen in the sand decreases and carbon dioxide increases; when a tide falls some oxygen is sucked in, but the amount depends upon size of sand particles and consequent pore volume for percolation. In fine sands capillary water inhibits marked changes but in coarse sands at high levels aeration may at times be good. Most beach animals probably are able to endure low oxygen tensions. Among microscopic types nematodes and ciliates live deeper than other animals. Larger animals that live in deep burrows have special arrangements for creating respiratory currents. Animals are variously adapted to withstand the beating and pulling action of waves and currents. Some (Venus, Cardium) are so heavy-bodied that they are not easily moved and, with some ability to burrow, they can hold their places. Other beach combers are rapid and skillful burrowers and dig in quickly no matter how often they may be turned out by waves. Most sand beach animals can survive exposure to the desiccating action of air. Soft animals such as Thyone and Paractis do not die when left exposed on sand. They lose water and shrivel more or less, which perhaps keeps their temperature lower when exposed to a hot sun. Most psammobionts escape unfavorable conditions by burrowing or migrating.

Microfauna.—Our examinations of salve box samples show (Table 4) that an abundant fauna of microscopic animals lives in sand beaches down to depths of 3-5 cm. The commoner types are nematodes, copepods, foraminiferans, polychaetes, burrowing amphipods (Haustorius), young clams, and flatworms. Nematodes are generally distributed on and in ocean bottoms. They often live in soils and bottoms where there is low oxygen tension, putrefying materials, and more or less of other substances that would make an environment unfavorable for many animals. Their small size and threadlike form enable them to move about among sand granules and their impermeable cuticle gives them ability to tolerate various undesirable solutes in the medium around them. Sand-dwelling copepods have been named terraqueous by

Wilson (1935). In his admirable descriptions he has pointed out that these crustaceans (Fig. 3) are (1) usually minute in size (0.25-0.5 mm. long); (2) have slender form; (3) flexible body; (4) great "tactile equipment and sensibility," especially on the antennae; (5) short antennae that curve back close to the head; (6) legs with few or no plumose setae but armed with spines for digging; (7) ovisacs flattened, closely appressed to the body, and with few, large
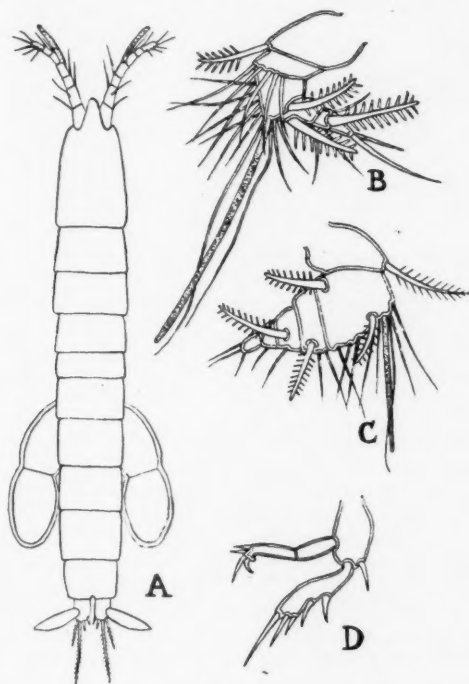

Fig. 3. Anatomy of terraqueous copepods from Wilson (1935). A, dorsal view of female *Goffinella stylifer*; B, first antenna of female *Rathbunula curticauda*; C, first antenna of female *Echinocornus pectinatus*; D, first leg of *Emertonia gracilis*.

eggs; and (8) limited ranges of movement, so that a species may have quite local distribution. They differ markedly from free-swimming, commensal, or parasitic copepods in structure and habits. Other burrowing crustaceans of somewhat larger size have some similar adaptations. Amphipods (Haustorius, Pontharpina) and isopods (Chiridotea, Cyathura) have poorly developed swimming organs and appendages modified for digging. One minute flatworm, *Archiloa wilsoni*, was often seen in salve box samples. It was very slender, flexible and active. It often looped along somewhat like a leech, by alternately attaching its posterior sucker and anterior end, or swam about when washed out of sand.

In sand beaches on the shores of lakes Pennak (1939) found rotifers, copepods, tardigrades, gastrotrichs, and nematodes were the prevalent animals. Of these only copepods and nematodes were found in marine beaches. Tressler (1940) says of the ostracods we collected at Beaufort, "These ostracods, while extremely small, are too large to exist between sand grains and probably were left by the tide or were found resting on sand when samples were taken in shallow water. The family Cytheridae, to which all these forms belong, is composed of strictly bottom dwelling ostracods which possess no power of swimming."

Coloration.—Most sand beach animals lack pigment and patterns. The ghost crab (Ocypode) is so called because its monotone blends with sandy surfaces and makes it difficult to see as it scurries about at night or on cloudy days. The beach "flea" (Talorchestia) shows similar coloration and habits (Smallwood 1903). Many psammobiotic crustaceans and molluscs are white, tan, or cream-colored (Haustorius, Emerita, Albunea, Ogyris; Venus, Spissula, Tellina, etc.). However, there are several that have large flecks or bands of brown, red, or other colors (Albunea, Ovalipes, Callinectes; Donax, Cardium, Macrocallista, etc.). Certain flounders at Beaufort are of course remarkable for their ability to match the colors and patterns of bottom backgrounds (Mast 1916).

Sense Organs.—Many sand beach crustaceans have very small eyes and compensate by having an unusual equipment of tactile organs. One might arrange a graded series from swift, aggressive crabs such as Callinectes and Aranaeus to setose, small-eyed, long-antennaed types such as Emerita or Lepidopa. Ogyris (Fig. 12) is unusual among sand beach crustaceans in that it has long eyestalks and large eyes, somewhat like those of fiddler crabs (Uca). Most specialized burrowing crustaceans have small eyes and are very setose. Burrowing annelids often have long tentacles on the head or other regions, but many lack such organs. Clams may have papillae on siphons or mantle. Burrowing snails usually have a long siphon which serves not only for respiration but also as a sense organ.

Locomotion.—The animals on sand beaches fall into two groups, those that have good powers of locomotion and hunt over bottoms (birds, ghost crabs, portunid crabs, squids, silversides, killifishes, etc.) in air or water and those that are poor swimmers but good burrowers and are more or less sedentary (sand dollar, heart urchin, Emerita, Albunea, Cardium, Donax, rays, flounders, burrowing eels, etc.). Arthropods with their stiff exoskeletons usually can run about or burrow in air or water. Some that have come from land, such as water-striders and certain flies, have their legs provided with a velvety coating of fine setae so that they are able to walk about on water. Tiger beetles and dolicopodid flies breed in sand beaches at Beaufort. Snails crawl over sand by secreting slime and thus making a firmer track. In the ocean, swimmers such as certain fishes, shrimps, and portunid crabs forage over beaches when they are immersed but are eliminated from areas that falling tides expose. Most specialized beach animals are poor swimmers and walkers but can burrow well.
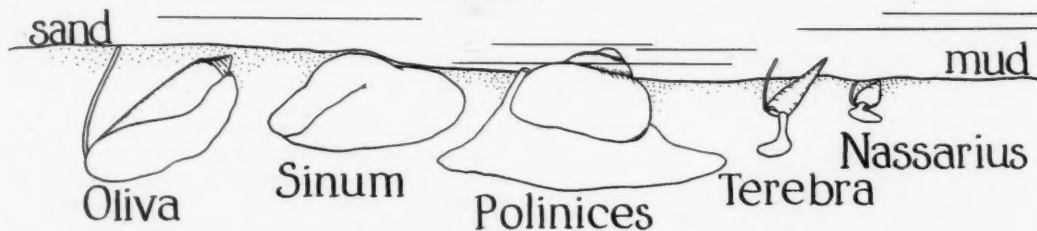
FIG. 4. Burrowing gastropods at Beaufort, N. C. Drawn under direction of Hulda Magalhaes.

There are some exceptions: the big clam, Cardium, can jump; Ogyris (Fig. 12) is a good burrower, but has a shrimp-like form and swims well; some good swimmers (Callinectes) burrow quickly and well.

Burrowing.—The burrowing habits of littoral sand beach animals are various. An anemone such as Parectis burrows slowly straight downward by making the aboral end small in diameter then enlarging it by slow peristaltic waves. The sea urchins, Moira and Mellita, also move almost directly downward by rapidly waving their spines and tube feet so as to move sand from underneath their tests toward the margins; then move it from the margins so as to cover the upper surface; neither sea urchin makes progress anteriorly as it descends. Moira on July 12, 1941, when placed in water on clean sand covered itself completely in 12 minutes. Small specimens of Cucumaria when placed in water on sand did not attempt to burrow but Thyone (Pearse 1908) moved straight downward by making its body narrow below and passing peristaltic waves lengthwise to move the sand, and covered itself in 2-4 hours. Leptosynapta burrowed by using the tentacles at the anterior end and peristaltic waves along the body wall.
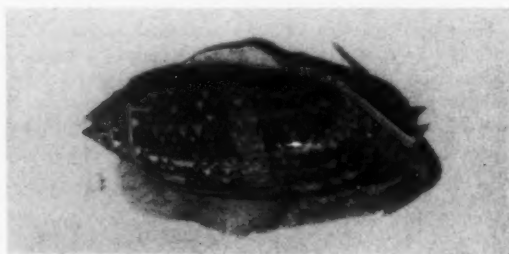
FIG. 5. *Oliva sayana* crawling on porcelain with siphon, tentacles, and foot extended. Photograph by Hulda Magalhaes.

Burrowing gastropods (Fig. 4) at Beaufort fall into two groups. (1) Those that have a very broad foot, secrete much slime, and plunge directly into wet sand (Polynices, Oliva, Olivella, Sinum). These have smooth shells more or less enveloped by the mantle. Polynices has a smooth, spiral shell; Oliva has a shiny shell shaped like a torpedo (Fig. 5),

which readily penetrates sand; and Sinum has its small shell completely enveloped by the wide, flat, slimy mantle (Fig. 4). (2) Snails that have large or spinose shells (Busycon, Terebra, Nassarius, etc.) burrow more slowly, and much as clams do; they poke the foot down into the sand as a slender wedge, then enlarge the end, and pull the body downward by shortening the foot. A specimen of *Busycon carica* in water on sand on July 18, 1941, covered itself completely, except for the tip of its siphon, in 12 minutes. A speedy burrower (Oliva, Figs. 5, 6) covered itself in 1 minute, 30 seconds on August 25, 1941. *Olivella mutica* burrows as well as its larger relative. Both go down quickly many times their own length below the surface; often so deep that their siphon cannot protrude.

All pelecypod molluscs observed burrowed by forcing their foot as a slender wedge into sand, expanding the end, and shortening the foot to pull the body downward (Fig. 8). Among them little Donax was speediest in its natural habitat. In loose sand where waves were moving it often buried itself with one insertion, expansion, and pull of its foot. Solemya, another little clam often burrowed several times its length below the surface. Heavy clams (Venus, Cardium, Macrocallista) with short siphons did not burrow far below the surface and required many foot pulls to submerge the shell so that their posterior end barely protruded. Slender clams with long siphons (Ensis, Tagelus) burrowed quickly and well. They usually remained deep below the surface. *Tagelus gibbus* (Fig. 9) frequents dark sands that border on muddy bottoms. It remains buried at depths of 40-50 cm. below the surface and has separate openings through the sand for its two siphons. Spissula is a heavy-bodied clam with comparatively long siphons (body length, 4.5 cm.; siphons, 3 cm.).

About five types of macroscopic burrowing crustaceans were found on the Beaufort beaches (Fig. 10). (1) Portunid crabs (Callinectes, Aranaeus, Ovalipes, Persephona, etc.) that frequented sand beaches wiggled into sand backwards. Aranaeus was observed to flirt sand forward away from the body with chelipeds, wave legs 2-4 rapidly from median line laterally and leg 5 posteriorly and dorsally. It sank nearly vertically into the sand. Ovalipes used
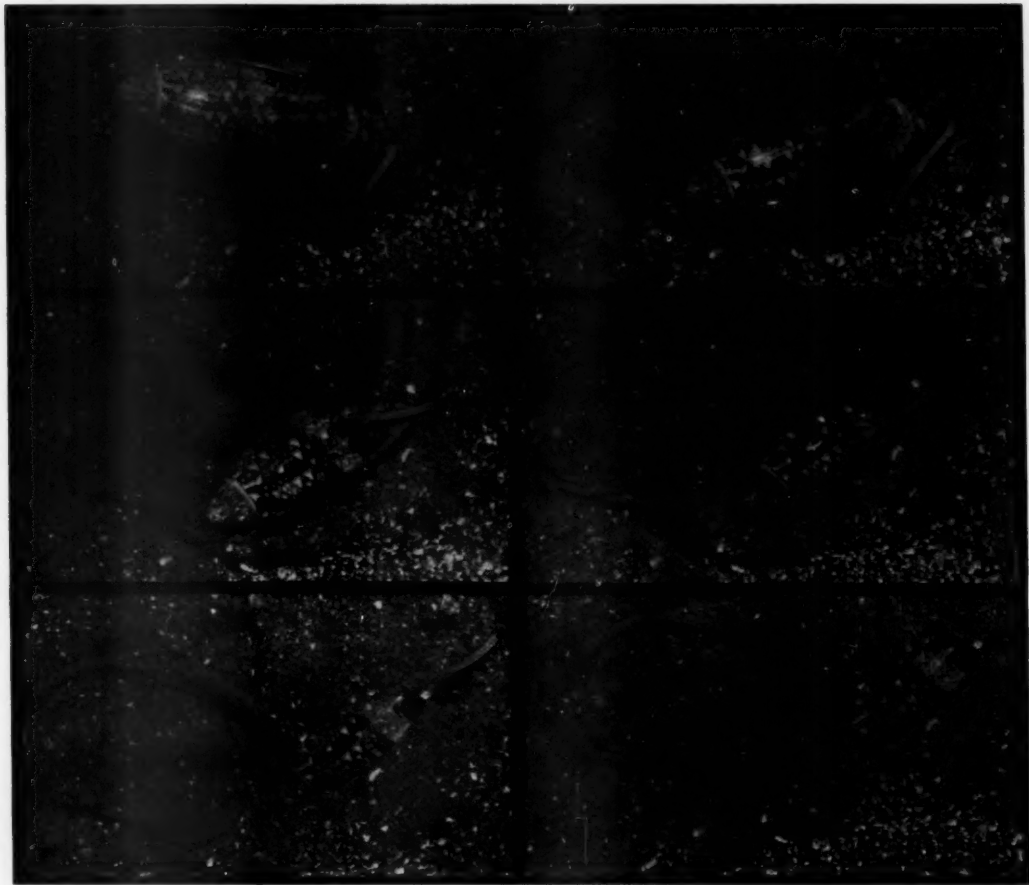
Fig. 6. Progress of *Oliva sayana* in burrowing. A, starting to burrow; B, after 15 seconds; C, 30 seconds; D. 45 seconds; E, 1 minute; F, 75 seconds, siphon withdrawn. Photographs by Hulda Magalhaes.

its chelipeds very little; waved legs 2-4 forward, legs 5 laterally and posteriorly, and descended nearly vertically. Callinectes burrowed much like Aranaeus but entered the sand at an angle, and not vertically. Aranaeus and Ovalipes often covered themselves completely, but Callinectes always rested with eyes, rostrum, and antennae protruding above the sand. A purse crab (Persephona) at once burrowed backwards; legs 2-5 were brought to the median ventral line and spread laterally. (2) The second group included expert and highly adapted burrowers with little ability as swimmers (Albunea, Emerita, Euceramus, Lepidopa). They have long antennae, short eyestalks and small eyes, inflexed abdomens, and legs adapted for digging by flattening and great spinosity. They burrowed backwards and at rest were at an angle with the surface with antennae extended into the water above, but if disturbed often descended several centimeters into the sand. Lepidopa is shown in Figure 11. In a later section of this paper (Fig. 22) Wharton describes the burrowing of Emerita in

detail. The amphipods, Haustorius and Pontharpina, fall in this group, but of course have no eyestalks; the latter has large eyes and does not burrow as deeply as the former. (3) Ogyris (Figs. 10, 12) was found to be peculiar, in that though it was a surface burrower like those in the last group, it had long eyestalks and a long abdomen. Furthermore, it burrowed head first by using its third maxillipeds and legs; sand was pushed upward and forward over the head; often the abdomen was left above the sand for a time, especially by ovigerous females. When digging leg 5 was held high on the sides and stroked dorsally and posteriorly; the swimmerets also stroked posteriorly; walking legs 1-4, laterally and posteriorly; maxillipeds, anteriorly and dorsally. (4) The two burrowing crustaceans (Calianassa, Lysiosquilla) that lived in more or less permanent burrows (Figs. 10, 13) that reached as much as a meter below the surface were quite different from other crustaceans. They had long, slender, soft bodies, short antennae,

FIG. 7. Progress of *Terebra dislocata* in burrowing. A, starting; B, after 5 seconds; C, 20 seconds; D, 30 seconds; E, 1 minute; F, 2 minutes. Photograph by Hulda Magalhaes.
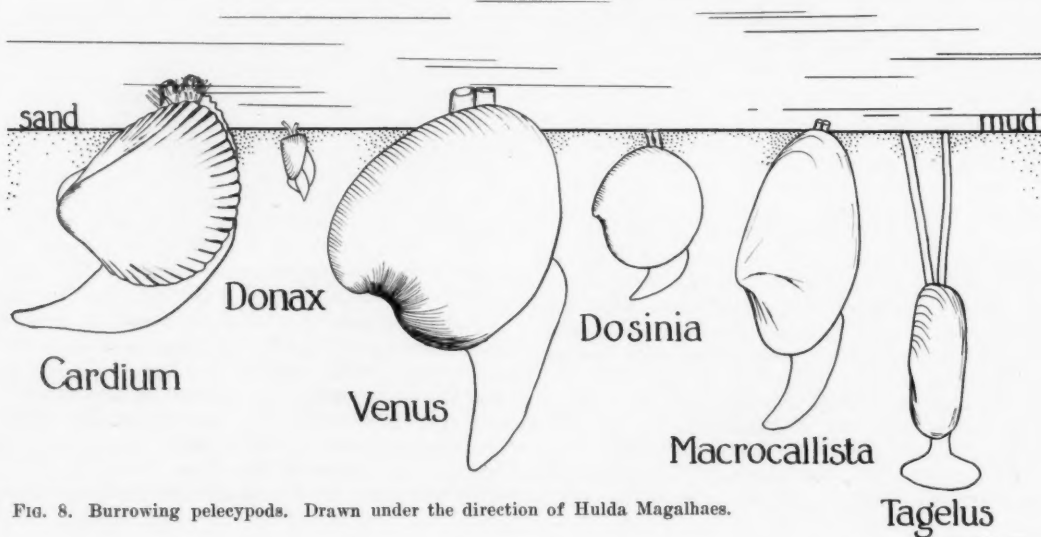
FIG. 8. Burrowing pelecypods. Drawn under the direction of Hulda Magalhaes.

and large abdomens with discoidal respiratory appendages. All walking legs were flattened at the tips, without claws, and very setose. When placed on clean sand under water both dug down head first at an angle. Once established in a burrow they often turned around and brought sand to the surface. The walking legs were used in burrowing by Calianassa and loads were carried and pushed ahead or dragged along with the chelipeds. Mac Ginitie (1934) and Lunz (1937) have given detailed descriptions of Calianassa's burrowing activities. Both it and Lysio-
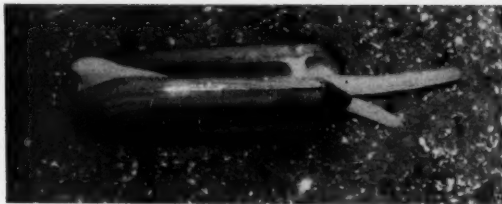
Fig. 9. *Tagelus gibbus* on sand with foot and siphons partly extended. Photo by Hulda Magalhaes.
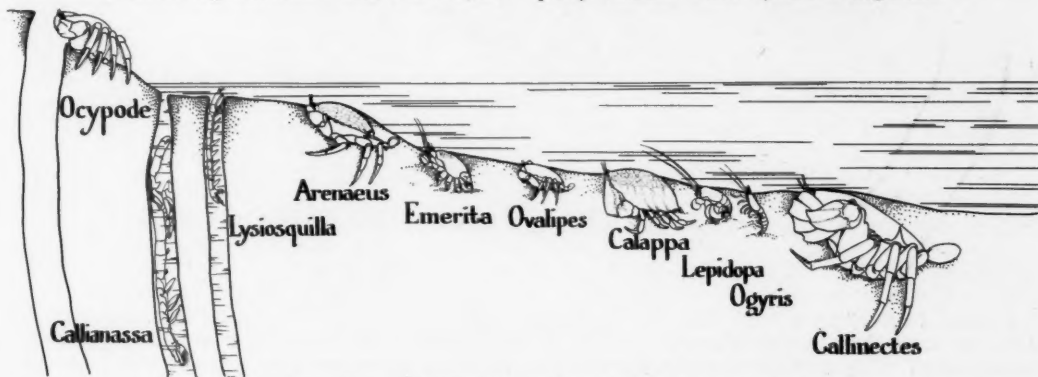
Fig. 10. Burrowing crustaceans in resting positions at surface of sand.

squilla lined their burrows with brown material that prevented caving in to some extent. (5) Chiridotea is very flat and though somewhat setose did not differ markedly from other isopods. It burrowed forward and usually rested just below the surface.

Burrowing chordates were not extensively studied at Beaufort. The lancelet, *Branchiostoma virginiae,* was very active. It dived instantaneously head first in sand by active wiggling when disturbed and often left part of its body exposed. It easily moved about beneath the surface of loose sand. Flounders, rays, sea robins, star gazers, eels, and other fishes commonly bury more or less of their bodies in the sands at Beaufort.
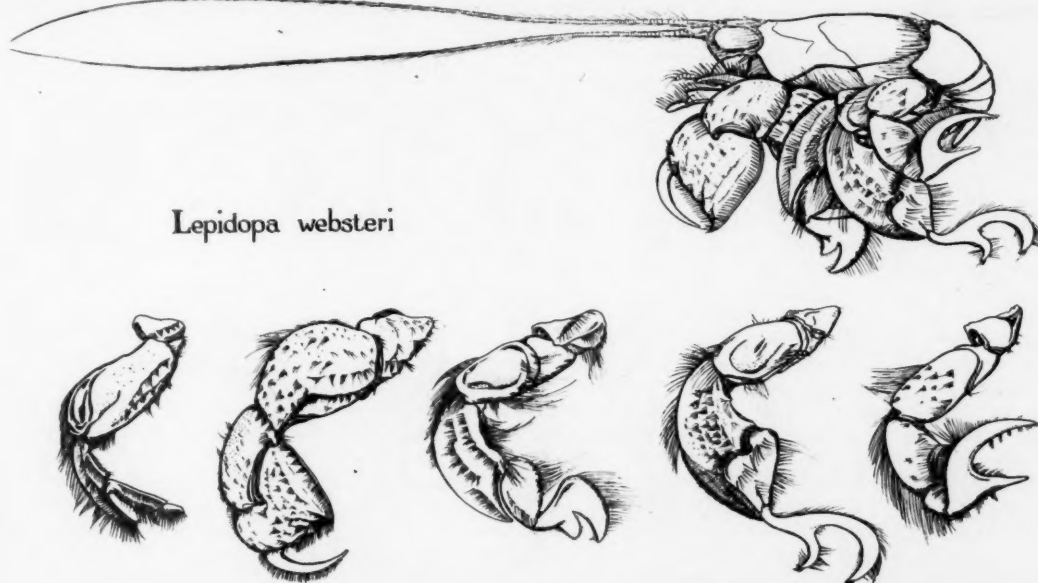
Lepidopa websteri

Fig. 11. *Lepidopa websteri*, a burrowing crustacean. Walking legs are shown in order from left to right.
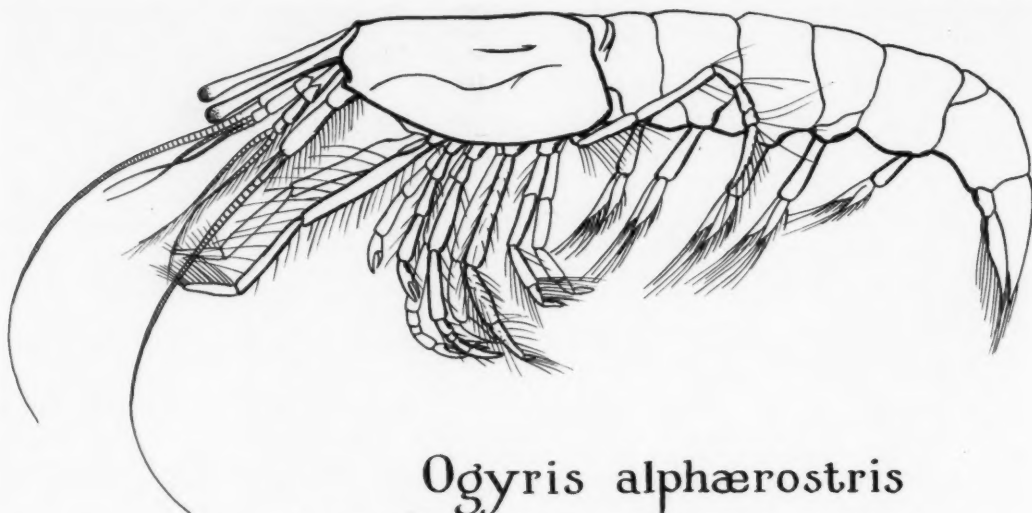
Ogyris alphærostris

FIG. 12. *Ogyris alphaerostris*, a burrowing shrimp.

Feeding Habits of Sand Beach Animals.—Although a marine sand beach at first glance appears to be rather barren of food there is plenty for animals that know how to secure it. The littoral water usually swarms with plant and animal plankters, there are numerous small organisms in the sand itself, and the flotsam and jetsam cast up by waves furnishes resources for scavengers. The portunid crabs and schools of little fishes that move inshore with every rising tide know that food is to be obtained there. Sipunculids are good examples of sand-dwellers that subsist on bacteria. Mac Ginitie (1932) studied the feeding habits of *Urechis capuo.* This sipunculid feeds by spinning a slime net that ensnares minute organisms. Two worms that were fed nothing but a culture of bacteria (*Pseudomonas* sp.) grew more during 68 days than controls kept under natural conditions. Another sipunculid *(Dendrostoma zostericola)* feeds on "organic sands" (Peebles & Fox 1933). At Beaufort Grave (1902) studied the feeding habits of three sand-dwellers. A spatangoid *(Moira atropos)* used its ambulacral brushes to pass bunches of sand and diatoms to its mouth. An ophiuroid *(Ophiophragma wurdmanii)*, "lives below the surface of sand with the oral surface of its disc and arms applied to some large object and with the
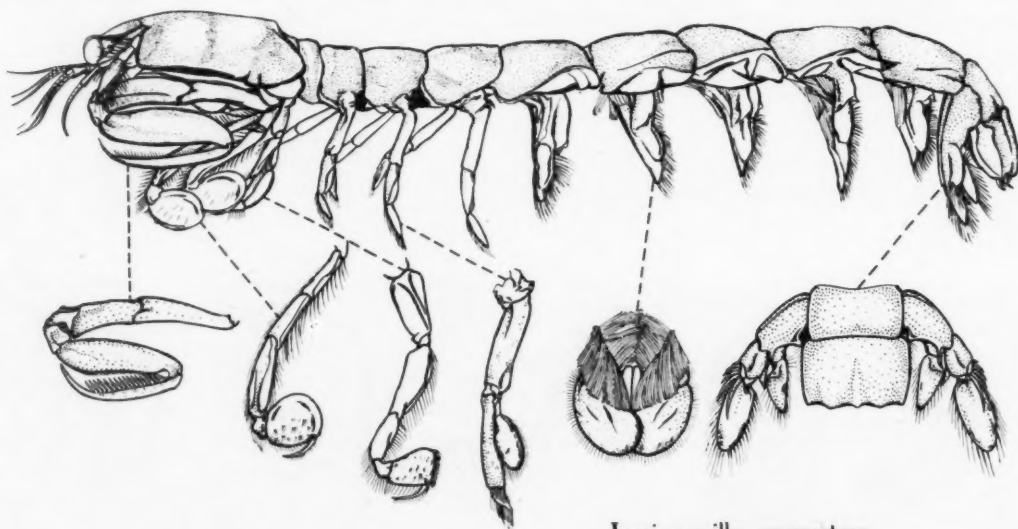
Lysiosquilla excavatrix

FIG. 13. *Lysiosquilla excavatrix*, a stomatopod that lives in a more or less permanent burrow.

tips of its arms extending into the water above. The foot-tentacles, distributed in pairs along each arm, are seen to be in constant waving motion, and by close observation it may be seen that they are busily engaged in passing little pellets of sand and diatoms toward and into the mouth." A holothurian *(Thyone briareus)*, "extends its oral tentacles, mops them about over the sand until they are well covered with sand grains and diatoms; then they are, one by one, turned back and poked down the throat; the mouth closes round the base of the tentacle and when 'withdrawn, it is free from all debris." Some worms (Amphitrite, Cirratulus) feed in a similar manner. Terraqueous copepods feed on diatoms (Wilson 1935), and on bacteria also (Clark & Gellis 1935). *Calianassa californiensis* sifts sand for contained detritus by using the brushes of setae on legs 2 and 3, the maxillipeds remove such food and transfer it to the mouth. At Beaufort *Calianassa major* has similar habits; its enteron contains little sand but is filled with fine brown organic debris that contains bacteria and diatoms. There are some worms (Balanoglossus, Arenicola) at Beaufort that apparently pass large quantities of sand through their alimentary canals without much selection of food; at every low tide numerous piles of fecal strings may be seen on the sand flats.

Among psammobionts there are several that feed by spreading setose nets to sweep plankters from flowing water. Emerita does this by extending its antennae above the sand and spreading the plumose setae on them. When the antennae are coiled beneath the head the setose mouth parts scrape food from them and transfer it to the mouth. Emerita's mandibles are reduced and non-masticatory (Weymouth & Richardson 1912). Other burrowing crustaceans with long antennae and setose mouth parts have more or less similar-feeding habits (Lepidopa, Euceramus, Ogyris, Haustorius, etc.). Some sand-beach crustaceans (Pinnixa, Pinnotheres, Polyonyx) are net-fishers, but live in the tubes of worms (Chaetopterus, Arenicola, Amphitrite) or the burrows of crustaceans (Calianassa) and even in the mantle cavities of molluscs (Atrina). Sand-burrowing clams (Cardium, Venus, Spissula, Dosinia, Macrocallista, Donax, etc.) feed by siphoning water through their mantle cavities and capturing the plankters in it.

Among the animals that seek food on sand beaches there are several scavengers. Ghost crabs at night collect about the carcasses of dead animals, much as vultures do during the day. The beach "fleas" (Talorchestia, Orchestia) live largely on the remains of stranded plants but at times devour dead animals also (Smallwood 1903). The snails belonging to the genus Nassarius *(N. obsoleta, N. trivittata, N. vibex)* prefer animal food but readily feed on plant remains (Dimon 1905). On any sandy beach at Beaufort numerous dolichopodid, asilid, and other flies are to be seen. These feed on bird feces, stranded algae, and other organic remains.

There are numerous carnivores that hunt over sand beaches. These range from protozoans and little plankton catchers, to porpoises, sting rays, and sand sharks. The common little fishes that follow rising tides are silversides (Menidia) and killifish (Fundulus). Others, such as lizard fish (Synodus), flounder (Paralychthys), and kingfish (Menticirrhus), are also often present. Portunid crabs (Callinectes, Arenaeus, Ovalipes, etc.) commonly hunt on rising and falling tides. On inundated beaches certain carnivorous worms (Glycera, etc.) come out of their burrows to seek food. Crustaceans such as snapping shrimps (Crangon) and hermit crabs also become active. Stomatopods (Lysiosquilla) sit at the mouths of their burrows (Fig. 10) ready to snatch up any passing animal that is fit for food. At times *Callinectes sapidus* may be seen running out of the water to pick Emeritas out of sand. When a beach is left bare, it is invaded by plovers, sandpipers, willets, grackles, buzzards, and gulls. These comb the sands for Donax, Emerita, clams, snails, and other animals. Tiger-beetles and robber flies also commonly forage on exposed beaches.

Breathing.—Animals that inhabit marine sand beaches usually must carry on their metabolic activities in a medium that contains little or no oxygen and more carbon dioxide than sea water. In any bottom made up of fine sedimentary particles, marine or freshwater, oxygen decreases and carbon dioxide increases rapidly below the surface. Mud bottoms are generally more deficient than sand, but both lack oxygen. Burrowing animals commonly have special adaptations for respiration. Snails have a long siphon (Fig. 6, 7) which protrudes through the sand into the water above. Clams that rest near the surface (Cardium, Venus, etc.) have short siphons, but those that burrow deep (Tagelus, Mya) have respiratory and feeding tubes that are frequently longer than their bodies. Crabs that remain near the surface (Calappa, Callinectes, Arenaeus, etc.) draw water in around the lateral and posterior margins of the carapace and pump it out at the anterior end. Callinectes has four anterior exits for respiratory currents. Arenaeus has a heavy coat of hair-like setae on either side of its mouth parts; this keeps out sand and, with the chelipeds held close against the front of the body, leaves a clear passage for currents from the branchial chamber. Ovalipes is unique in that it has respiratory currents passing in through anterior lateral openings and out through two posterior openings; when one is buried beneath the surface two little vortices that appear just behind its body show where water leaves. Emerita when buried extends its antennae and draws currents in through the canal that the setae on the antennae enclose; but the current may often pass in the opposite direction (Weymouth & Richardson 1912; Mead 1917). Slender crustaceans (Callianassa, Lysiosquilla, Fig. 10) that live in more or less permanent burrows have several pairs of swimmerets adapted to form discoidal pumping organs; these beat continually and force currents through their burrows. Sometimes their underground dwellings

have two openings to permit the ready entrance and exit of water.

Reproduction.—At Beaufort the most active periods of reproduction for beach animals are during spring and summer, but some spawn more or less at all seasons. On the coast of Great Britain Arenicola breeds from February to April (Ashworth 1904); at Beaufort spawning occurs somewhat throughout the year; on December 6, 1941, several egg strings were observed and some examined under a microscope contained developing eggs. In spring Limulus appears on the flats and males may be seen riding about attached to females throughout the summer. Once a small male was found attached to a larger male. Emeritas and copepods also have males attached to females during the breeding season. Some burrowing shrimps also consort in pairs (Crangon; Mac Ginitie 1937). In a shifting medium like a sand beach such behavior helps insure fertilization. In July and August blue crabs and Emeritas are often carrying eggs. In summer abundant snails, such as *Nassarius obsoleta*, often are to be seen copulating (Dimon 1905). Sand molluscs generally pass through a swimming veliger stage before settling down. Figure 14 shows developmental stages of a Calianassa. Beach worms produce enormous num-
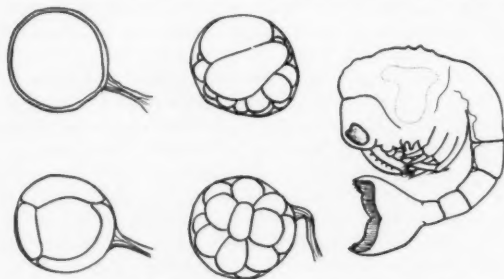
Fig. 14. *Calianassa major;* egg, segmentation stages, and larva.

bers of eggs; copepods that live in sand produce very few (Wilson 1935); crustaceans and molluscs that have free-swimming larvae produce many eggs and have rather long breeding seasons. For example, ovigerous Emeritas may be found during 4 or 5 months in summer. Some sand beach animals (Emerita) are annuals, others live for several years. Churchill (1919) states that the average life of a blue crab (Callinectes) is three years; both sexes become mature in one year, after 15 to 20 molts, and mate, but do not spawn until the second summer after they hatch. Mac Ginitie (1934) believes that Calianassas live several years.

Enemies.—Beach animals usually escape enemies by burying themselves, and many small animals will descend several centimeters if disturbed. However, there are some predators that are expert at extracting buried psammobionts. Plovers and sandpipers leave holes along beaches at every low tide, where they probed with their beaks for Emerita, Donax, and other small buried animals. Gulls and oyster catchers

pick clams out of beaches and fly to rocks or paved roadways, where they drop them so as to break the shell and gain access to the soft body within. Such hard-shelled molluscs as Venus, Area, and Ostrea are thus destroyed. When tides rise fishes, crabs, and creeping starfishes forage over beaches. There are also small consortes that invade the burrows of larger animals. At Beaufort *Pinnixa cristata* lives in the burrows of worms and crustaceans. On the coast of California Mac Ginitie (1934) found seven species of animals living in burrows of Callianassa.

SEASONAL PROGRESSION ON SAND BEACHES

Conditions on Beaufort sand beaches vary somewhat with the annual cycle of seasonal changes. During most of the year prevailing winds are from the southeast; but in the autumn they become northeasterly.

Shore birds change with seasons. In summer terns and laughing gulls are dominant but in winter thousands of herring gulls sit about on beaches and deposit considerable organic material as feces. In early summer there are few cormorants in the Beaufort sounds and estuaries but after these birds have reared their broods they are common on harbor beacons and along the beaches. In summer there are more shore birds (such as sandpipers, plovers, godwits, grackles, etc.) hunting alongshore than during winter. Blue crabs (*Callinectes sapidus*) are common and aggressive everywhere along sand beaches, but in winter are quietly resting in bottoms in deeper water.

Wharton's work (p. 157) on Emerita has shown that crustacean to be an annual. Young are produced
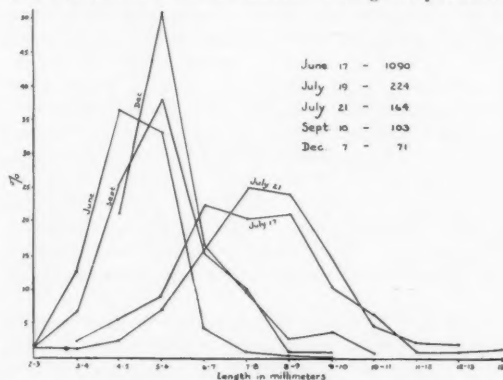

Fig. 15. Length of *Donax variabilis* shells on beaches near Fort Macon, 1941.

in summer and the adults then die off before winter comes. In the autumn and winter there are many little Emeritas in beach sands. Our observations on a small beach clam (Donax, Table 9, Fig. 15) indicate that it is also an annual. Though less complete, data on a little snail (Olivella, Table 10) indicate the same. Small individuals are more numerous during and after the breeding season in summer and large

TABLE 9. Lengths of *Donax variabilis* shells from Fort Macon beaches, in millimeters; sifted from sand, 1941.

Date	No. exam.	Max.	Min.	Ave.
June 17.....	1090	9.5	2.1	4.8
July 19.....	224	13.0	3.0	5.8
July 21.....	164	12.5	2.3	7.6
Sept. 10.....	103	10.0	2.5	5.4
Dec. 7.....	71	9.0	4.1	5.7

TABLE 10. Lengths of *Olivella mutica* shells in millimeters; picked up by hand, 1941.

Locality	Date	No. exam.	Max.	Min.	Ave.
Sheepshead Shoal.....	June 20	76	15.0	4.6	8.9
Sheepshead Shoal.....	July 2	51	13.0	5.0	8.5
Sheepshead Shoal.....	July 4	94	12.2	4.7	8.9
Sheepshead Shoal.....	July 8	43	13.0	4.3	8.9
Shackleford Bank.....	Aug. 7	30	11.0	2.4	7.9
Ft. Macon Beach, inside.....	Dec. 7	5	7.4	6.1	6.9

individuals decrease after that time. Large beach crabs (Callinectes, p. 153) and molluscs (Cardium; Johnstone, 1899; Venus, etc.) may breed during the next summer after they begin life, but also breed in two or more succeeding summers. Most beach animals are actively breeding during summer and are more or less inactive, metabolically and ecologically, during colder months.

A TYPICAL SAND BEACH ANIMAL, THE MOLE CRAB, *EMERITA TALPOIDA* (SAY)
By George W. Wharton

The early stages in the life history of *Emerita talpoida* were studied by Smith (1877). His excellent paper is recommended for a detailed account of the morphology of immature stages. Weymouth & Richardson (1912), Mac Ginitie (1938), and ZoBell & Feltham (1937-38) have investigated the habits of *Emerita analoga*, which occupies the same habitat on the Pacific coast of the United States as *E. talpoida* does on the Atlantic coast. For the most part the two species of crustaceans have similar habits. However, certain differences do occur.

EGG

The eggs of *E. talpoida* are a bright orange when first laid. They are attached in usual decapod fashion to the long hairs of the mother's pleopods. As development proceeds the color gradually fades until just before hatching they are a translucent dirty gray.

During the summer of 1940 several collections of *E. talpoida* were made (Table 11). On June 2 only

TABLE 11. Collections of Female Emeritas.

Date	No. with eggs	No. with small males	Total
1940			
June 2.....	43	0	292
July 25.....	22	0	25
July 28.....	103	0	104
July 29.....	13	0	13
August 3.....	12	3	16
August 7.....	25	11	37
August 16.....	61	34	97
August 18.....	76	24	105
August 20.....	38	46	88
August 24.....	7	22	32
August 27.....	25	27	53
August 30.....	14	38	53
December	0	0	7
1941			
June 28.....	33	0	54
December 7.....	0	0	17

43 of 292 females were ovigerous; by July 25, 103 of 104 females were found with eggs attached to the abdominal appendages; only 14 out of 53 females collected August 30 bore eggs; and in December of 1940 and 1941 no ovigerous females were found. Likewise no females with eggs were found in a collection of 17 females in May, 1941. Those observations indicate that the egg laying season is roughly June through September in the region of Beaufort, N. C.

The eggs upon hatching liberate a first stage zoea larva.

ZOEA

Numerous attempts at towing, sieving with a fine mesh sieve, and examining sand with the aid of a binocular microscope, turned up only a single zoea. That one was taken in a tow net in the surf off the outside beach of Fort Macon on June 2, 1940. The larva had recently hatched since it was still in the first stage. Smith (1877) found and described four zoea stages. They are easily recognized by the conspicuous lateral spines and lack of a dorsal spine. The first zoea stage not only lacks the dorsal spine but the two laterals as well. First stage larvae are easy to obtain during the summer, since the females with eggs about ready to hatch will yield large numbers if brought into the laboratory. Several attempts to keep the first stage larvae until they moulted met with failure.

MEGALOPES

The megalops larvae of *Emerita talpoida* occur in large numbers in the sand which is washed by the waves. The most efficient method found for collecting this stage was to dig a hole in the sand above the water's edge and then to strain with a tow net the water swept into the hole by waves.

The megalopes are amphibious like the adults. They are well adapted to burrowing in the sand and swimming in the surf. In habit and structure they closely resemble the small adults. The simplest way to separate the megalopes from the other stages in

a collection is to place the living animals in sea water. The megalopes swim actively about with the abdomen extended, so that their peculiar biramous pleopods (Fig. 16A) can be used with effect. The young adults swim with the abdomen flexed and the telson tucked between the thoracic appendages.
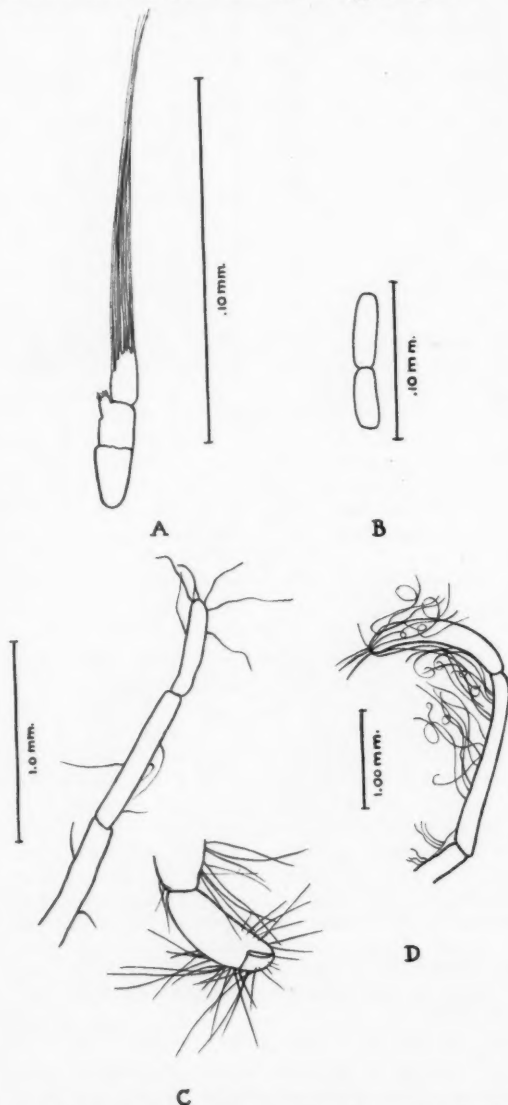
hairs offer considerable resistance to the water. The endopodite has quite another function. The tip of this tiny knob is set with many small hooklets which engage the hooklets of the endopodite of the opposite side. This arrangement joins the paired appendages in such a way that they work as one. There are four pairs of pleopods in the megalops stage.

During the summer of 1940 no megalopes or young adults were found until July 29. From July 29 until the last collection on August 30 the relative numbers of megalopes and young adults varied considerably (Table 12).

TABLE 12. Collections of small *Emerita talpoida* in the summer of 1940.

Date	Megalopes	Adults 4 mm. and under
Before July 29............	0	0
July 29...............	3	16
August 7................	124	53
August 10................	195	34
August 16................	36	323
August 20................	238	57
August 24................	53	82
August 27................	43	120
August 30................	4	33
Total..........	696	718

About a month and a half elapsed between the appearance of females with eggs and the appearance of megalopes and young adults on the beaches. This lag in time probably represents the period of development from the laying of eggs until the young return to the adult mode of life.

The megalopes have an even distribution over the beach. They are found between tide marks in the wash of the waves just as the larger adults are, but they do not form colonies.

YOUNG ADULTS

No method of determining the sex of the larval stages was found. In fact it is not known whether the sex of larvae is determined. All of the megalopes examined were identical with respect to the pleopods and the third and fifth thoracic legs. This is not true of the young adults however. The sexes, though superficially very much alike, can be separated by the examination of the appendages. The males have no pleopods and the basal segment of the fifth leg is expanded at its distal end. Likewise on the females the genital opening (Fig. 23B), which is absent in the males, can be made out on the coxae of the third thoracic appendages even in the very small individuals.

The young females during their first summer were found in the same areas with the megalopes and were collected in the same manner. The development of the pleopods of the female was studied (Fig. 16). The earliest condition noted was a pair of biramous pleopods on each of the first four abdominal segments. These consisted of an exopodite of one seg-

FIG. 16. The first pleopod of various stages in the development of *Emerita talpoida:* A, megalops; B, female, 4 mm.; C, female, 9 mm., also tip of fifth leg; D, female, 20 mm.

The pleopods of a megalops are truly swimming appendages. They consist of three segments, a basal piece, a large, flat, hairy, paddlelike exopodite, and a small knob-shaped endopodite. The exopodite is adapted for swimming. Its wide blade and long

ment, an endopodite of one segment, and a single segmented basal piece. The exopodite was larger than the endopodite, but the difference was in no way as striking as the condition found in the megalops. This earliest stage was observed only once. The next stage was observed to have four pairs of single segmented pleopods. Following this the posterior pair of pleopods was lost, leaving three pairs of 1-segmented appendages. Later stages were found which had one pair of anterior 2-segmented pleopods followed by two pairs of 1-segmented pleopods. These females had a carapace length of 4 mm. (Fig. 16B). The 5 mm. carapace females had the first pair of abdominal appendages uniramous and 3-segmented, the second pair 2-segmented and the third pair 1-segmented. Females with a carapace length of 7 mm. had the first two pairs of pleopods uniramous and 3-segmented while the posterior pair was 2-segmented. The females with a carapace length of 8 mm. and above had three pairs of uniramous 3-segmented pleopods (Figs. 16 C, D). The number of hairlike setae increased as the size of the pleopods increased. The length of the pleopods decreased posteriorly in all cases; the first was largest, the last smallest.

From the first summer after hatching until the following May the average carapace length of females increased from 3 mm. to about 8 mm. (Table 13).

TABLE 13. Average length of carapace of *E. talpoida* yearling females.

Date of collection	Carapace length in mm.	Date of collection	Carapace length in mm.
1940		1940	
June 2.....	11.1	Aug. 27....	16.6
July 25.....	15.8	Aug. 27....	18.6
July 28.....	16.3	Aug. 30....	18.8
July 29.....	14.3	Dec.	4.3
Aug. 3....	11.1	1941	
Aug. 7.....	16.8	May 28....	8.0
Aug. 18.....	17.6	June 28....	11.4
Aug. 20.....	18.0	Dec. 7....	5.0

The small males which make their appearance on the beaches at about the same time as the small females (Table 14) have an interesting habit. They are sexually mature, and they seek out and attach themselves to the year-old females. The sperm sac on the basal segment of the fifth leg is filled with mature sperm (Fig. 17). As many as seven of these miniature consortes have been found on a single large female. Many cases of male parasitism are known among Crustacea. The condition of the small males of *Emerita talpoida* is probably an incipient parasitism. The mating habits of *E. analoga* were studied by Mac Ginitie (1938). He reports no such activities of small males as was found in *E. talpoida*. However, he does mention that some of the larger males cling to the females for 2-5 days. The method by which these small males feed is as yet unknown. That they remain attached for long periods is evi-

denced by the fact that small males are collected only rarely by the method used for the megalopes and small females.

The attachment of the small males to the large females is achieved by various methods. These semi-parasitic mates have been found in the gill chambers, clamped between the coxae of the thoracic appendages, attached to egg masses, clamped by means of their telson to the ovigerous hairs of the pleopods, and some seem to roam about on the ventral surface of the larger females. A few males seemed to be attached by means of the spermatophores which are
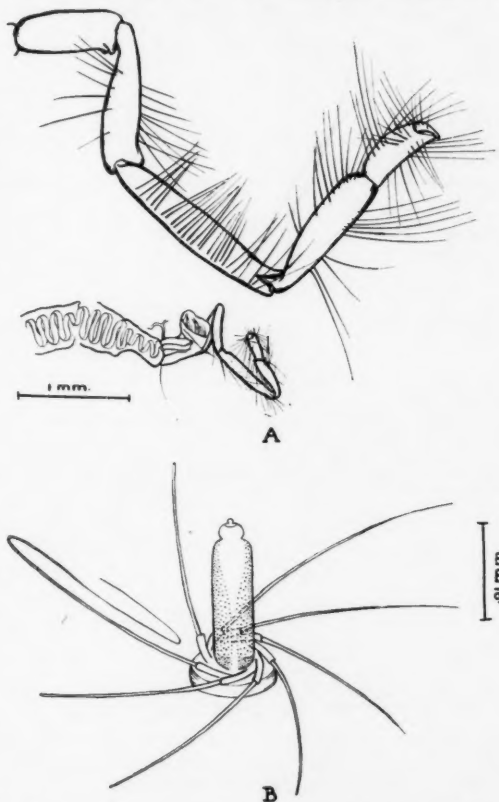

FIG. 17. Fifth leg and sperm of males. A, fifth leg showing vas deferens and sperm sac; B, mature sperm.

extruded from the basal segment of the fifth leg; however, these may have been merely depositing the spermatophores. In all cases involving the spermatophores the attachment was made between the coxae of the fourth thoracic appendages of the females.

The usual carapace length of the small attached males was 3 mm. They had small stumps or buttons at the point where the pleopods were attached in the megalops stage, but in no case was a pleopod observed on a small male. In the larger males not even a trace remains of the pleopods.

During the fall the large host females to which the small males are attached disappear from the

beaches and by December they are not to be found in the Beaufort area. Their consortes, however, do not pass out with them but again assume a free living existence. In December, 1940, and December, 1941, the number of males and females collected were about equal (Tables 14, 15). December is the earliest

TABLE 14. Collections of Male Emerita. Length of carapace of largest male was 14.0 mm.

Date	Number of free living	Av. carapace length of free living	Number attached
1940			
June 2.....	112	6.7	0
July 25.....	34	7.8	0
July 28.....	6	7.7	0
August 3.....	0	...	3
August 7.....	4	8.8	14
August 16.....	8	9.6	62
August 18.....	3	8.5	31
August 20.....	7	8.1	77
August 24.....	1	8.0	43
August 27.....	7	7.8	64
August 30	3	10.6	72
December	5	3.8	0
1941			
May	3	9.0	0
December 7.....	15	5.3	0

TABLE 15. Frequency of Carapace Lengths of Females; 1940.

Length of carapace in mm.	Number of individuals	Length of carapace in mm.	Number of individuals
7	15	17	151
8	37	18	138
9	51	19	106
10	61	20	43
11	44	21	17
12	32	22	11
13	16	23	4
14	25	24	2
15	61	25	0
16	99	26	1

time that an approximate 1:1 sex ratio was obtained for individuals of the same generation by the same collecting method. In the summer the young females made up the bulk of the young adult catches, and the bulk of the old adult catches. By December about half the catch was male and about half female. It is unreasonable to suppose that enough young females died off to make up the discrepancy. The numbers on the beaches dictate against this hypothesis. A store of males must have been added to the population in the sand. This store was available only from the stock which was associated with the large females during the last half of the summer and early fall.

From the time of the appearance of the small males on the females in August until the following June they increase in carapace length from an average of about 3 mm. to an average of about 7 mm. (Table 14).

GROWTH OF LARGE FEMALES

A study of the increase in the length of the carapace was made on large females during the summer of 1940 (Table 13). During the summer of 1941 numerous *E. talpoida* were measured for carapace length by Pearse and Humm but no distinction was made between males and females. Likewise no record was kept of the megalopes, small females, and small males; so that the measurements give a picture not so much of the growth of *E. talpoida* as they do of the sizes of the population as a whole at the time and location where the collection was made.
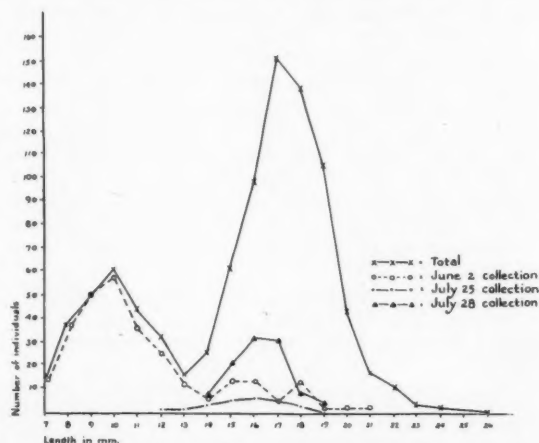
FIG. 18. Carapace length frequency of *Emerita talpoida* collected during the summer of 1940.

The largest female was collected on August 16, 1940, and had a carapace length of 26 mm. Females of this size are very rare in the Beaufort region. Nine hundred and fourteen large females 7 mm. and over were collected during the summer of 1940 and measured (Table 15, Fig. 18). The most frequent carapace length observed was 17 mm. The frequency curve is distinctly bimodal with one mode at 10 mm. and the second at 17 mm. This is explained by the fact that no collections were made from the first week in June until the last week in July. By the last week in July until the end of August the average carapace length was close to 17 mm. but in June when a large collection was made the average carapace length was only 11.1 mm. Figure 18 illustrates this graphically.

Three of the 1941 collections (Table 17, Fig. 19) were characterized by bimodal frequency distributions according to carapace length, while two were not. The June 4, 1941, collection has a frequency distribution of carapace length distorted by the presence of males included with the females. The July collections show a bimodal frequency because the young adults have been included with the year-old *E. talpoida*. The September collection for some reason does not include the young Emeritas and is therefore not bimodal. The collecting method might

account for this. The mode of the yearling Emeritas increased from 9 on June 4 to 15 on September 10, 1941.

The 1941 crop of *E. talpoida* was considerably (about 3 mm.) smaller in carapace length than the
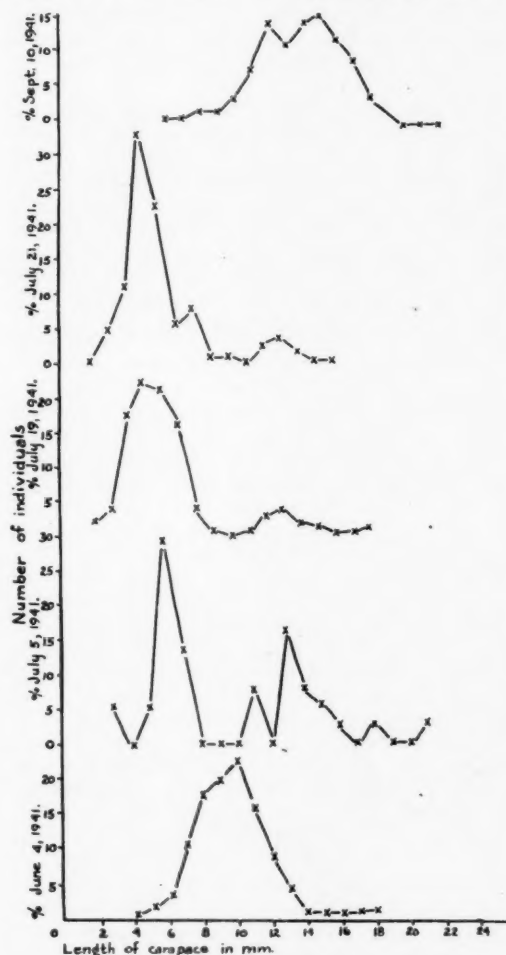
1940 crop. During the summer of 1940 the average carapace length increased from 11.1 mm. on June 2 to 18.8 mm. on August 30 (Table 13, Fig. 20). The increase appears to have been linear throughout the growth period with no tapering off at the older limits. For this particular growth period *E. talpoida* increases in carapace length at the same rate, 0.08 mm. per day, regardless of size. Such a growth rate is unusual. However, this rate is not maintained

FIG. 19. Carapace length frequencies of 1941 collections.

TABLE 16. Length vs. Width of Carapace of Females; 1940.

Length, mm.	Width, mm.	Length, mm.	Width, mm.
7	5.0	17	12.7
8	5.7	18	13.5
9	6.3	19	14.1
10	7.0	20	14.8
11	7.7	21	15.7
12	8.5	22	16.6
13	9.0	23	17.3
14	10.7	24	18.7
15	11.1	25	....
16	11.9	26	18.8

TABLE 17. Collections of Emerita, 1941.

Date	Length of Carapace, mm.			Frequency of Carapace, Length, mm.		Number Collected
	Average	Smallest	Largest	1st year mode	2nd year mode	
June 4...	9.42	4	18	..	9	516
July 5...	9.48	3	21	6	13	37
July 19...	6.20	2	18	5	13	227
July 21...	6.08	2	16	5	13	206
Sept. 10...	13.98	6	22	..	15	412
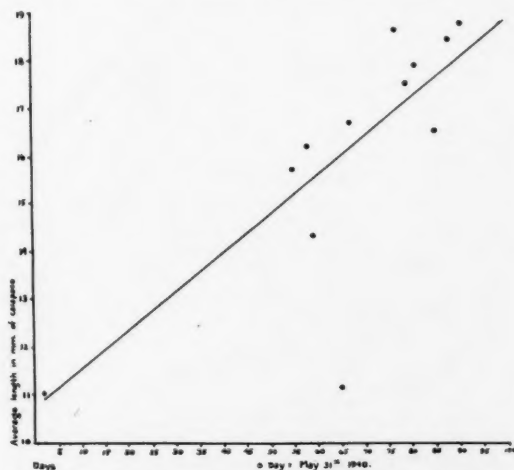
FIG. 20. Increase of carapace length with time during the summer of 1940.
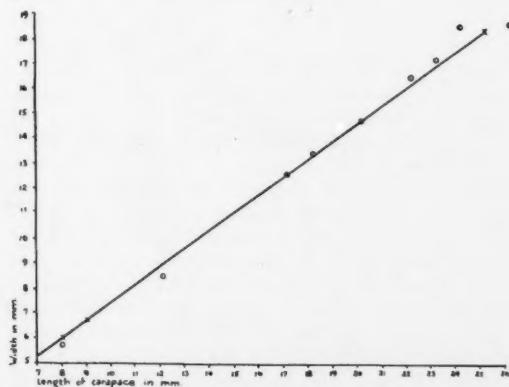
FIG. 21. Carapace width vs. length. Line is theoretical; length is 1.35 times width.

throughout life but is slower during the early stages of development.

The relative growth rates of length and width of carapace were compared (Table 16, Fig. 21). It was found that the carapace length was about 1.35 times the width from 7 mm. to 26 mm. This of course indicates that the shape of *E. talpoida* does not change with increasing size.

GROWTH OF LARGE MALES

The yearling males seem to increase in size during the summer months (Table 14). However, the most notable characteristic of the large males is that the majority of them die off in July. On July 25, 1940, of 59 *E. talpoida* collected 34 were males. In all later collections there were far fewer males than females. It is interesting that just as the number of yearling males decreases the new crop of small parasitic males is ready to take on the job of fertilizing the females.

ADAPTATIONS OF *Emerita talpoida*

A mole crab lives in a precarious environment. The physical difficulties imposed by the shifting sands and beating waves coupled with the exposure to predators from land and sea make it impossible for unspecialized animals of any size to live on sand beaches between the tide marks. *E. talpoida* is a specialist in two things: (1) burrowing and (2) straining.

The large, coiled, setose antennae are so constructed as to enable it to strain a living from the water of receding waves. Weymouth & Richardson (1912), Mac Ginitie (1938), and ZoBell & Feltham (1937-38) have studied the feeding habits of *E. analoga* on the Pacific coast. The antennae of that mole crab are in fact such effective nets that even bacteria fall prey to them. The feeding habits of the two species are very similar except that *E. analoga* is not as dependent upon wave action for straining water as is

FIRST LEG

THIRD LEG

UROPOD

FOURTH LEG
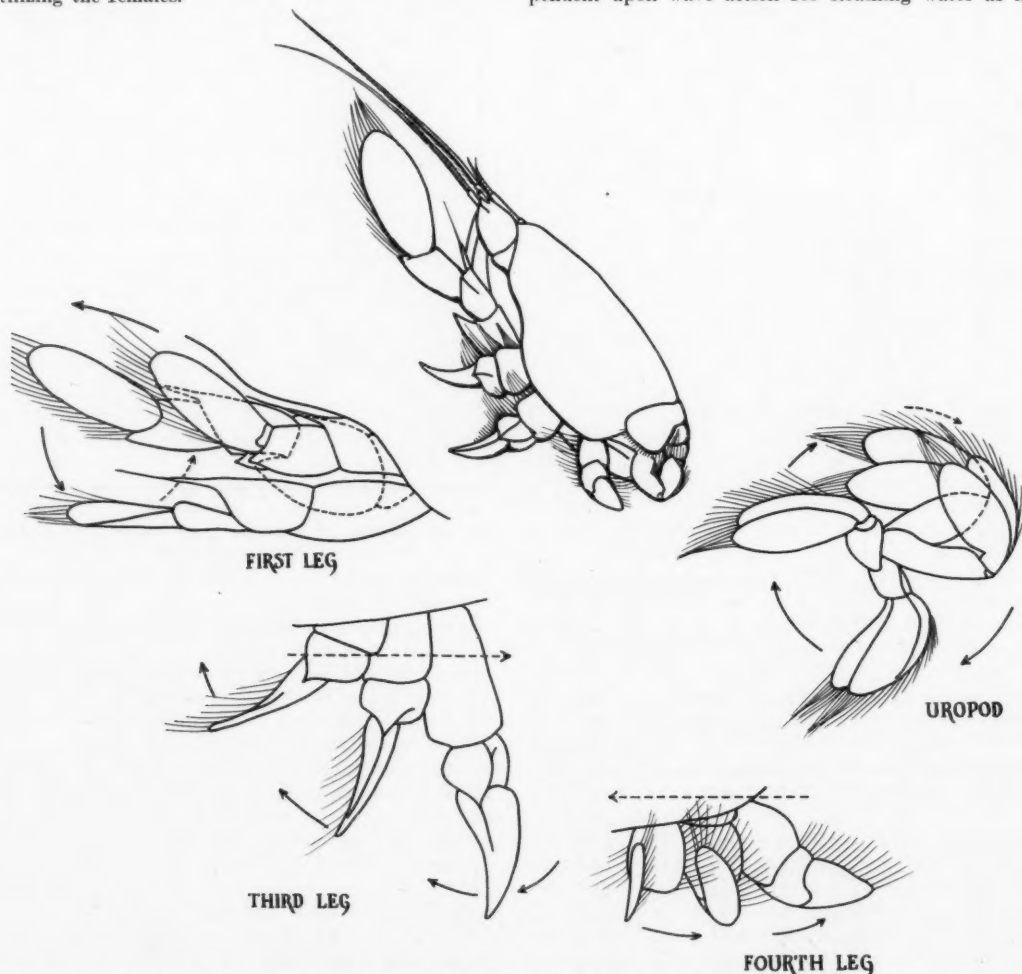
FIG. 22. Resting position of *Emerita talpoida* in the sand, and diagrams to show the movement of the appendages while burrowing. Solid arrows indicate power stroke. Dotted arrows recovery.

E. talpoida. Numerous attempts to keep *E. talpoida* in quiet waters failed. At times it was noticed that *E. talpoida* would wave its antennae through quiet water, but no food was found in the stomach of specimens of *E. talpoida* kept in a large tank of running sea water even though small waves were made to wash an artificial beach in which the Emeritas were buried. ZoBell & Feltham (1938) on the other hand kept and fed bacteria to *E. analoga* in quiet water in the laboratory. They report that the crabs cleaned up the bacteria by waving the antennae actively about in the water. *E. talpoida* usually strains the water only as it is receding. The reason for this seems to be a mechanical one. The antennae are constructed to stream out in front of the animal and since *E. talpoida* faces the ocean the incoming wave would bend the antennae over the back of the animal and perhaps break them off. All of the water of the receding wave is not strained. Only the last half of the water when the depth over the animal is two inches or less is searched for food.

E. talpoida can swim but it is not particularly adapted to this mode of locomotion. As mentioned previously the megalops has its pleopods well developed for swimming, but in adults these appendages are lost in the males, and specialized to carry eggs in the females. The uropods are the most effective appendage in the swimming of adults.

E. talpoida is specialized as a shallow burrower. Its resting position in the sand is shown in Figure 22. The coordination of its appendages while burrowing has been worked out. When it is preparing to burrow, it backs up to the wet sand. Dry sand or moist sand is too hard for *E. talpoida* to burrow in. The uropods rotate in unison in such a manner as to throw the sand dorsally on top of the animal while forcing the posterior end into the sand. The small fifth thoracic legs do not come into play in the burrowing. The fourth thoracic legs move in unison laterally and posteriorly. The third and second thoracic legs have the same movement. Working in unison they move the sand anteriorly and force the posterior end of the body into the sand. The first pair of thoracic appendages work alternately to push the sand laterally and anteriorly. Such alternate action makes it appear as though the animal were wriggling into the sand. The appendages all move in such a manner that the recovery is along the line of least resistance, and the effective stroke is made with the flat face at right angles to the plane of the direction of the movement. The hairs of the burrowing appendages are also arranged to give maximum resistance during the power stroke.

The fifth thoracic leg (Fig. 23A), while it does not assist in burrowing, is important. It is tucked up inside the gill chamber and, with its sub-chelate hand and numerous long hairs, functions to keep the gills clean.

The general shape of *E. talpoida* as well as its apronlike telson are such that burrowing is easy.

The mating habits of *E. talpoida* in late summer which entail the small attached males are ideal for
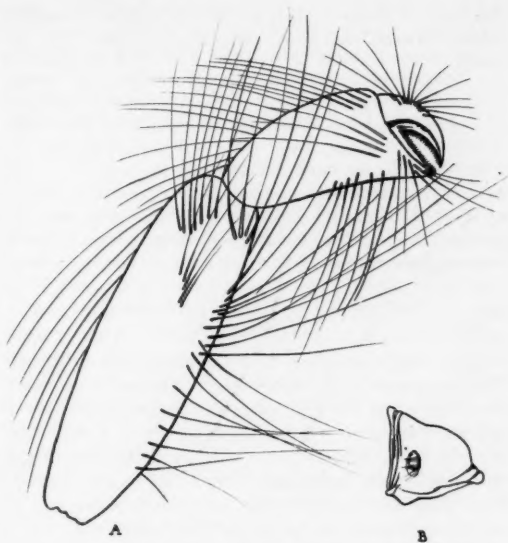

FIG. 23. A, end of fifth leg of female; B, female genital opening on the third coxa.

an animal which lives in a turbulent environment. By this means the female can live undisturbed during the process of copulation. In the late spring and early summer copulation must be carried on between the large males and females. Copulation of the large males was not observed. One peculiarity however was noted which might have some bearing on the mating of the yearling males. During the first week in June of 1940 only a few *E. talpoida* were captured on the beach. Numerous cast skins, however, were piled up on the drift line, and this indicated that large numbers of *E. talpoida* were in the vicinity. The use of a minnow seine solved the problem. Numerous males and females were swimming in the surf. Was this a nuptial swim? At no other time were Emeritas captured in large numbers in the seine. The genital opening of the male is at the distal end of the coxa of the fifth leg (Fig. 17A). The female genital opening is on the coxa of the third leg (Fig. 23B).

Another peculiar habit of Emerita is its social activity. Young Emeritas are not found in colonies but are evenly distributed over the beach. The large adults invariably congregate in large colonies that work together. If one of the colony leaves its burrow the entire colony is apt to follow it into the surf. In any given colony almost all of the individuals will extend their antennae at the same time. How these colonies are formed and kept together is still a mystery. It may be that the continuous distribution observed in the young is broken by unfavorable zones in which most of the animals die or it may be that in the spring the Emerita gather in favorable spots.

E. talpoida goes up and down the beach with the tide. It seems that movement is dependent upon

the flow of water. Mole crabs will follow a shallow wave towards the water and a deep wave up the beach.

DISTRIBUTION

E. talpoida is an inhabitant of steeply sloped, open beaches where the wave action is considerable. It was found to be most common on the outside beach at Fort Macon, quite common on the inside beach at Fort Macon and Shackleford, and very rare on the flat "inside" beaches of Sheepshead Shoal. Waves seem to be a necessity for it.

THE ROLE OF *Emerita talpoida* ON SAND BEACHES

The faunas of sand beaches constitute a climax formation in the Beaufort region, where ocean and land meet. In the establishment of this climax, wind and wave have played the dominant role. Even without life it is very probable that sand beaches would be formed, just as mountains and valleys are formed. It is difficult to imagine that any organic succession could occur on a beach, except that which might follow withdrawal of the water. If an area of beach were to be denuded of life, the void would immediately be filled by organisms from the surrounding areas. No orderly sequence of events would ensue.

Myriads of animals and plants have cut ecological niches for themselves into this ready-made environment. Plant life is largely unicellular. The animal life, however, is quite varied. The sand beach animals must have found a ready-made environment and adapted themselves to it through long evolutionary changes.

Emerita talpoida is so well adapted to its environment that it is incapable of making a living except in the intertidal zone of wave-swept sandy beaches. Of all the animals present, perhaps mole crabs are the most conspicuous. However it is highly improbable that they had anything to do with the formation of their environment.

The mole crab in its role as a plankton feeder is one of the important "fixers" of food on sand beaches. Fishes, birds, and carnivorous invertebrates use it for food. The rapid turnover and quick growth of *E. talpoida* make it an important source of flesh.

SUMMARY

The life history of *E. talpoida* is as follows. Eggs are laid and carried by the mature females throughout the summer months. Larvae hatch in the zoea stage, which goes through several moults and finally becomes a megalops. The first large crop of megalopes are found toward the end of July. The megalops moults into the adult. The young adult females live evenly distributed along the sands, as the megalopes do, but the young males attach themselves to large females and fertilize their eggs. During the fall, winter, and spring young adults increase in size. Females by June average about 10 mm. in length and males which have abandoned their consortes reach an average length of about 7 mm. in

the same time. In the early summer the females which have reached egg bearing size (10 mm. and over) are fertilized by the large yearling males. The majority of the large males die off in the middle of the summer. The females carry eggs until late summer and all die before the following winter. The males live for about one year and have two periods of active reproduction. The females live about a year and three months and have only one active reproductive period.

The habits and structure of *Emerita talpoida* are well adapted to a life in the intertidal zone of wave-swept sand beaches. It is an important plankton feeder on sand beaches and thus "fixes" food for the larger carnivorous animals.

PLANTS OF BEAUFORT SAND BEACHES
BY HAROLD J. HUMM

INTRODUCTION

An ecological survey of sand beaches would contain serious gaps without a study of plants concerned in their economy. With this fact in mind, a certain amount of detailed attention was given the flora of Beaufort sand beaches during the summer of 1941.

Most botanists regard a typical ocean beach as a habitat that is barren and infertile. In the past, sand beaches have served botanists interested in marine algae only as a place where good collecting prevails after a storm has torn loose such plants and washed them ashore. Occasionally, accumulations of microscopic plants in tidal pools have been such that they were readily seen and collected. But to the unaided eye, the really important flora of ocean beaches is invisible and its study requires special techniques.

In so far as time and the extensive scope of this problem would permit, those techniques were employed, limited by the investigator's own shortcomings, and a study was made of bacteria and algae.

Algae are divided into two groups: macroscopic species which wash ashore and decay, and microscopic species indigenous to or at least living in beach sand of the intertidal zone. An attempt was made to understand the role of bacteria through application to beaches of work done by others on marine species living in ocean water and ocean bottom. In addition, a quantitative study was made.

It is hoped that this preliminary survey will indicate a few of the many problems associated with sand beaches that await the attention of specialists.

ROLE OF BACTERIA IN THE ECOLOGY OF BEAUFORT SAND BEACHES

A beach is an important place where organic material is reduced by bacterial action to an inorganic state. Marine organic matter may be divided, arbitrarily, into three types: (1) that which is so finely divided that it remains in suspension indefinitely, either in solution or in colloidal form; (2) that which tends to sink and is decomposed on the bottom; (3) that which is sufficiently buoyant and macroscopic so

that it tends to be washed ashore. This latter type is being washed up onto sand beaches constantly in amounts which vary with direction and force of winds, tide levels, amounts of rainfall, and other factors. The organic content of beaches is further augmented by the droppings of shore birds, by a small amount of vegetative material washed or blown in from dunes, and by such finely divided organic material as is brought in by waves and retained by the sand as water percolates through it.

There are reasons for believing that organic decomposition by bacteria goes on at a greater rate after material has been cast up onto a beach and while tides are low than while it is still in the water. This increased bacterial activity in sand which has an adequate moisture content probably is influenced by the following factors: bacterial enzymes become concentrated upon and around organic particles in absence of diluting effects of water; rapid multiplication of bacteria follows and these are not washed into suspension until the next high tide; higher temperatures prevail in intertidal sand at the surface on clear, summer days when the tide is low than when it is high; there is a greater availability of oxygen at the surface of sand exposed to air; and, in the case of algae and many animals, death usually does not occur until after they have been washed up and exposed. Thus there is an endless cycle of washing up of organic matter by wave and tidal action and a dissolving out, especially at high tide, of organic and inorganic decomposition products resulting from bacterial action. Decomposition products do not accumulate in typical ocean beaches but are returned to the sea and probably contribute to the higher concentrations of nitrates and phosphates near shore.

Bacterial activity in sand beaches, as in the sea, is important in three principal respects: (1) organic matter is reduced to inorganic; (2) inorganic matter is transformed, including reduction of nitrates and probably nitrification; (3) bacteria serve as food for small animals. Clark & Gellis (1935) have shown that bacteria serve as food for copepods. Other small animals found in sand, as reported in another part of this paper, including nematodes, flatworms, protozoa and amphipods, probably use bacteria as food.

Much excellent research has been done during the past ten years on the role of marine bacteria in the cycle of life in the sea by Waksman, ZoBell, and others. The findings of these workers frequently apply, in principle at least, to the intertidal zone as well as to ocean water and ocean bottoms.

THE NITROGEN CYCLE
Nitrogen Fixation

The presence in the sea of *Azotobacter chroococcum* Beijerinck and the anaerobic *Clostridium pasteurianum* Winogradsky, apparently identical with land strains of these species, was first demonstrated by Benecke and Keutner (1903). That they are normal inhabitants and active nitrogen-fixers in this habitat was also shown by these workers. Later both species

were isolated from many different parts of the sea. Thus the only two non-symbiotic bacteria which bacteriologists generally agree are active nitrogen-fixers in soil are active also in the sea. Apparently no attempt has been made to compare amounts of nitrogen fixed in the two habitats.

Nitrification

That nitrification takes place in sand beaches is indicated by the work of Issatchenko (1908) who found more bacteria which oxidize ammonia to nitrites or nitrites to nitrates in sandy bottoms and shell-rich bottoms than in mud. Waksman, Hotchkiss, & Carey (1933) found that sea water, especially the upper layers, contained very few nitrifying bacteria but that they are active in ocean bottoms. Carey (1938) showed that bottom material produced nitrite when inoculated into standard media containing ammonium salts, and that this was oxidized later to nitrate. The latter process took place more slowly. Nitrifying bacteria, though scarce in water, were shown to be present in concentrated copepod, dinoflagellate, and diatom tow, as inoculations of this material into media that contained ammonium salts gave nitrite production. Nitrate production did not follow, however.

In view of the fact that ocean bottom often contains millions of bacteria per gram as compared to only a few hundred, or often less than 100 in ocean water remote from sources of terrestrial contamination, it is not surprising to find that special physiological groups of bacteria are much more difficult to demonstrate in ocean water than in bottom material. A given type could be relatively more abundant in water than in mud and be much more difficult to find in the former. It would be interesting to know what percentage of total populations of bacteria in both places are nitrifiers.

Because large numbers of saprophytic bacteria constantly are releasing ammonia as a decomposition product in ocean beaches, it is not unreasonable to believe that nitrification occurs there as well as in sandy ocean bottoms. Apparently this activity has never been studied in intertidal zones.

Denitrification

Denitrifying bacteria were found in the sea bottom by Waksman, Hotchkiss, and Carey (1933). These authors conclude that the activities of such bacteria are so limited by a number of environmental factors that they do not seriously reduce supplies of nitrate in the sea. Of 30 different cultures isolated by the present writer in the process of making bacterial counts of sand beaches, only 10 reduced nitrates to nitrites. The majority produced ammonia. One, to be studied further, may be a denitrifier.

AGAR-DIGESTING BACTERIA

While working in Beijerinck's laboratory, H. H. Gran (1902) discovered bacteria which digest agar through the production of an enzyme which he called "gelase." He also discovered the iodine reaction as

a test for agar decomposition. Since that time, only a few detailed studies have been made of species capable of digesting agar. The most important are those of Lundestad (1928), Gorseline (1933), and Stanier (1941). Although a few terrestrial and freshwater species have been isolated and described (Panek 1905, Biernacki 1911, Gray and Chalmers 1924, Aoi and Orikura 1928, Nicol 1931, Gorseline 1933), the majority have been found in the sea. Most of those isolated from soil or freshwater appeared accidentally in connection with investigations on cellulose-digesting organisms.

Marine algae, especially Rhodophyceae, constitute the commercial source of agar. Although a considerable number of chemical investigations have been made on agar and several empirical formulae proposed, its composition is still imperfectly understood. It is a complex hemicellulose which, like cellulose, is highly resistant to hydrolysis. Czapek (1922) stated that it is one third galactan and contains pentosans.

In the past, bacteriologists have generally regarded agar as an inert constituent of their media, added solely to give a semi-solid consistency. Recently, however, agar has been shown to contain various "growth substances" (Robbins 1939). It probably contains traces of all the commoner compounds of the sea and it is doubtful if any amount of washing or soaking in distilled water will reduce the concentration of these "impurities" to a point where they will not be significant.

Because of its complexity and because of the various ways different species of agar-digesting bacteria attack it (complete hydrolysis leaving pits and depressions, liquefaction, or merely softening), it is likely that the enzyme "gelase" is an enzyme complex and that various agar-digesting organisms produce different combinations of the constituents of "gelase." It is possible that those which only soften agar, changing its iodine reaction, produce but a single agar-hydrolizing enzyme which acts upon only galactan or upon a single pentosan. Apparently no studies of this enzyme system have been made.

More cellulose-digesting organisms have been reported and described than agar-digesters and, among the former, both aerobic and anaerobic types are found whereas all agar-digesters so far reported are obligate aerobes. There are probably many anaerobic agar digesters also. Are not marine algae decomposed anaerobically or at least under low oxygen tension?

Waksman & Bavendamm (1931) found from 50,000 to 200,000 agar-digesting bacteria per gram of mud in shallow ocean bottom in the Bahamas. These workers proposed an hypothesis which, if correct, places such bacteria, also common in intertidal sand beaches, in an extremely important ecological role. They suggested that possibly nitrogen-fixing bacteria live in symbiosis with agar-digesters and through this association growth of algae is possible in a medium as poor in available nitrogen as the sea. Their hypothesis includes the following propositions:

"The algae growing abundantly synthesize large quantities of hemicelluloses;

"The agar-liquefying and other similar bacteria decompose these hemicelluloses liberating large quantities of available energy;

"The nitrogen-fixing bacteria use this energy and fix nitrogen;

"The algae as well as the agar-liquefying bacteria use this nitrogen directly, or after the bacterial cells have autolized or undergone decomposition."

That such a cycle takes place on ocean bottoms and beaches is possible, but there is no experimental evidence in support of the suggested symbiosis. It seems that the energy rendered available may be used to a much greater extent by saprophytic bacteria because of their great numbers.

Fig. 24. Sargassum on beach at Station IV and V.

Regardless of whether agar-digesting bacteria are directly involved in the nitrogen cycle, there is no doubt that they constitute a very important physiological group in the intertidal zone and in ocean water and bottom. Algae are being washed ashore in small quantities constantly but after storms beaches are littered with tons of them. At Beaufort great quantities of pelagic Sargassum (S. natans, S. fluitans) are cast up (Fig. 24) or form endless driftlines six inches or more in depth. At other times the beach may be littered with green, red, and brown algae which grew attached. Since both groups are rarely mixed on the beach, they are apparently washed up as a result of different meteorological conditions. It is remarkable how quickly the last trace of such material disappears from a beach. Other saprophytic bacteria live in the debris with agar-digesters in great numbers and are benefited by the release of hexoses, pentoses, and other components of agar. This fact was seen in cultures where, in the presence of agar-digesters, other marine saprophytic bacteria grew more rapidly than they did on plates of the same medium (inorganic salts, agar, seawater) which lacked agar digesters. Not only did other saprophytic bacteria benefit, but many protozoans (monads, marine amoebae, mastigamoebae, etc.), marine species of Euglena and other one-celled, green algae, germinating spores of Enteromorpha

sp.; bluegreen algae; and many species of diatoms appeared in the cultures. Some organisms failed to develop except in the vicinity of agar-digesting bacteria. Many diatoms, some bluegreen and green algae, including Euglena and spores of Enteromorpha which grew into small (5 mm.) thalli that lived for several months, actually grew in liquefied agar. Although the agar medium had been slightly buffered with dibasic potassium phosphate, apparently the bacteria that digested the agar produced very little acid. Some species seemed to have brought about a complete hydrolysis of agar. Inoculum for these plates was prepared by adding beach sand to a beaker of seawater and pouring this mixture rapidly back and forth between two beakers until a substantial proportion of sand flora and fauna had been brought into suspension. Some of this suspension was streaked onto plates of 1.5% and 2% seawater agar to which only nitrate and phosphate had been added.

Stanier (1941) studied in detail seven species of agar-digesters isolated from the sea along the coast of California. His work throws additional light upon the importance of these bacteria as decomposers of organic debris. Of the seven, six also digested cellulose, three attacked alginic acid, and four hydrolized starch. None attacked chitin. Six required a source of organic nitrogen. Four either formed shallow depressions in agar or merely softened it. Three attacked it more vigorously causing liquefaction or deep pits.

Of three agar-digesters studied by Waksman, Carey, & Reuszer (1933), two attacked cellulose and two attacked starch.

Since time did not permit the making of a comprehensive survey of agar-digesting bacteria that occur in sand beaches at Beaufort, several were studied to a limited extent. Isolations were made from routine plate counts and from plates with diatom cultures. No attempt was made to secure additional species by means of enrichment culture media. A detailed study of those already isolated and efforts to find additional species will be made in the future.

One of the most common agar-digesters of the cultures on hand has been tentatively identified as *Flavobacterium rhodomelae* (Lundestad) Bergey *et al.* It produced bright yellow colonies which became orange or orange-brown with age and formed shallow, concave depressions in agar. Treatment with iodine revealed a wide gelase field around the depression.

Another culture possessed many characteristics in common with *Achromobacter litorale* (Russell) Bergey *et al.* Its ability to attack agar was not detected until the iodine test was employed. Agar is softened only, even if the agar percentage is barely enough to gel. Waksman, Carey, and Reuszer (1933) found that one of their organisms would attack agar if it were present in a concentration of 0.5% but not of 1% or higher. Apparently they did not make the iodine test on this organism. *A. litorale* (if the identification is accurate) does not visibly attack even as low a concentration of agar as 0.5%. The description of this species in *Bergey's Manual* does not mention digestion of agar. Starch is vigorously hydrolized, small amounts of hydrogen sulfide are produced. These characters also are not given in the description. No loss of agar-digesting ability was detected after six months in pure culture.

Two other cultures were of the rapid agar-digesting type. They formed a deep groove in peptone agar slants within 24 hours and produced pits to the bottom of Petri dishes within two days even in 2% agar. Both hydrolized starch. One important difference was the presence of a gelase field around each pit in one organism and the absence of such a field in the other as shown by the iodine test. Both digested agar in the presence of sucrose, starch, lactose, mannitol, and maltose, but did so very little or not at all in the presence of dextrose. Rates of agar digestion were slower when any one of the previously-mentioned sugars was present. Several other distinctly different species were isolated too late in the course of the work to permit a study of them.

CHITIN-DIGESTING BACTERIA

Bacteria that have the ability to digest chitin constitute another special group which has been investigated to a very limited extent. ZoBell & Rittenberg (1938) give an insight into the importance of these bacteria in the sea when they state that several billion tons of chitin are produced annually by copepods alone. They found up to 1,000 chitinoclastic bacteria per gram of sand on California beaches. As a result of mixed and pure culture studies, they make the statement that "observation on certain mixed cultures indicated that there are also symbiotic relationships in which two or more bacteria together can attack chitin although neither alone is endowed with this property." At present, digestion of chitin is determined by visual examination of purified pieces added to culture media. It is possible that some bacteria bring about a partial but invisible decomposition analogous to bacterial digestion of agar in which agar is merely softened. As yet, no chemical test for chitin decomposition which compares with the iodine test on agar has been utilized by bacteriologists. Thus when two species of bacteria together can digest chitin, but neither alone does so, it may be that they are producing enzymes which attack different constituents of the chitin molecule, either one of which does not produce visible decomposition.

ZoBell & Rittenberg (1938) report further that chitinoclastic bacteria which they isolated lost their chitin-digesting ability and their pigmentation upon prolonged cultivation on fresh-water media, and also became adapted to fresh-water media.

Hoek (1940) studied chitin-digesters extensively in the Woods Hole region. He found 60,000 per gram in a sandy bottom in shallow water and only about 125 per gram in a mud bottom. Further emphasis of the importance of sand over mud as a habitat for chitin-digesting bacteria is the fact that cleaned shells of horseshoe crabs (Limulus) lost three fourths of

their weight within a period of one year in sand, about one third in mud, and almost none in ocean water.

Although copepods are important chitin producers in Beaufort sand beaches and may considerably outnumber other groups of crustaceans, amphipods (Haustorius, Orchestia, Talorchestia) and decapods (Emerita, Callinectes, Ovalipes, Arenaeus, etc.) produce a great deal more chitin because of much greater size of individuals. Numbers of copepods found in Beaufort beaches are given in Table 4, of Haustorius in Table 5. Attempts to count or isolate chitin-digesting bacteria were not made.

BACTERIAL POPULATIONS

The Value and Accuracy of Counts

Some measurement of total population of saprophytic bacteria in sand beaches is of interest for purposes of comparison with counts made from sea-water, bottom, and cultivated soils. Such counts are also of value as a key to the importance and nature of bacterial activity in sand. Furthermore, it is necessary to have relative measurements of populations in various localities on a beach, and at different times, in order to determine what factors are most influential upon it.

There is no accurate method of determining total numbers of bacteria in sand, soil, or water. No one medium has been devised upon which all bacteria will grow. Counts are made usually of saprophytic bacteria because they are easiest to grow and generally most numerous. But even saprophytic bacteria cannot be counted accurately. Anaerobic types can be counted only by means of apparatus in which oxygen is removed or oxygen tension reduced. When such counts are made, both obligate and facultative anaerobes develop and thus these counts cannot be added to aerobic counts for total numbers of saprophytes because a considerable number of species will develop under both conditions of culture.

In any attempt to determine bacterial populations of soil or sand, difficulties are encountered which are not inherent in water counts. Most important are the fact that many bacteria tend to adhere firmly to sand and soil particles, and that continued shaking in water apparently kills some. The periphytic propensities of marine bacteria (ZoBell & Allen 1933, Hotchkiss & Waksman 1936, ZoBell 1936) are probably more pronounced than those of freshwater bacteria. Even if there were a really accurate method to determine numbers of bacteria per gram of beach sand, it would have a limited value because of fluctuation in numbers in response to ever-changing conditions. It is quite possible that the population of a given area of sand could double in an hour or two under favorable conditions, or be reduced to one half within the same period by a rising tide, a hard rain or some other environmental factor. Bacterial counts at best must be in terms of averages of many separate determinations.

Counting Methods

Four methods have been used to determine bacterial numbers in soil and water samples. The oldest and still most widely used is the poured plate method in which appropriate numerical dilutions of a sample to be measured are made with sterile water. Usually one cubic centimeter of a certain dilution is added to melted agar which has cooled to about 45° C. This is quickly poured into a sterile Petri dish. After incubation for about seven days, colonies are counted and calculations made. For greatest accuracy, the dilution must be such that from 40 to 200 colonies will develop on each plate (Waksman 1927). Jennison & Wadsworth (1940) have discussed errors involved in the plating method.

The direct microscopic method involves the same principle as a haemocytometer. A known amount of an appropriate dilution or an undiluted sample is placed upon a slide upon which it covers but one square centimeter. In one modification of the method, it is then oven dried, covered with a dilute solution of agar, fixed with alcohol, and stained. Counts are made of a number of small unit areas. Hanks & James (1940) have studied this method.

The dilution method consists of making a long series of dilutions (usually 10-fold) of a sample to be measured and inoculating nutrient broth in test tubes with a certain quantity of each. The highest dilution in which growth occurs is used to calculate the population of the original sample. Greater accuracy is obtained by inoculating two to ten or more tubes with each dilution. This method averaged 20% higher than plate counts of the same material (Gordon 1939).

A fourth method, introduced by Henrici (1933), was used at first to study freshwater and marine bacteria. It was later employed by Hotchkiss & Waksman (1936) in quantitative determinations and called the "attachment count" method. Sterile, clean slides are suspended in water for 24 hours or more and then fixed, stained, and counts made of unit areas. The periphytic habits of many bacteria, or tendency to adhere to solid surfaces, is made use of in this method. The significance of the numbers is determined first by comparing them with poured plate or direct microscopic counts of the same sample. ZoBell & Allen (1933) objected to the use of this method of counting as they showed that many species of marine bacteria do not attach.

Methods Used

Since the plate method of counting seemed to be best adapted to circumstances at Beaufort, it was used almost exclusively. Dilution and attachment count methods were tried occasionally.

In the plate method, one gram of sand was placed in 10 cc. of sterile sea water in a test tube and this was shaken vigorously exactly 100 times (about one half minute), substituting the cotton plug with a sterile cork stopper temporarily. One cubic centimeter of this suspension was then transferred to a tube containing 9 cc. of sterile sea water, and so on.

until the desired solution was attained. The contents of each tube was thoroughly mixed after each transfer. Dilutions which permitted counting were usually 1,000:1 or 10,000:1. In cases where a greater volume was needed, duplicate dilutions were made or 1 cc. of the original dilution was transferred to 99 cc. of sterile sea water in an Erlenmeyer flask. From four to eight or more plates were poured from each sample and an average count obtained.

According to Waksman (1927), soil samples should be shaken five minutes in the dilution water. A shorter time leaves a substantial number of bacteria clinging to soil particles which settle; a longer time seems to kill some bacteria. A few preliminary tests seemed to indicate that this does not apply as strictly to beach sand as it does to soil, in that bacteria apparently cling to sand grains with greater tenacity. Five minutes shaking still leaves a significant number adhering to the sand. Therefore it seemed advantageous to shake the tube 100 times, as uniformly as possible, and then attempt to calculate the average percentage of bacteria brought into suspension with this treatment, if an idea of total numbers of saprophytic aerobes was desired. It was believed that this method would be just as accurate for relative measurements, and there was a saving of time.

Simple arithmetical calculations only were made in determining numbers per gram. Because there are so many sources of error which cannot be mollified by statistics, the figures were not subjected to such an analysis.

In order to determine approximately what percentage of aerobic, saprophytic bacteria, measurable with the medium employed, were removed from one gram of sand when shaken 100 times in 10 cc. of sterile water, the procedure was as follows: After dilutions from the original 10 cc. of water had been made, it was poured off and a new, sterile 10 cc. added. The sand was again shaken 100 times and similar dilutions made, several of which were plated. The water was again poured off the sand and another sterile 10 cc. aliquot added. This procedure was repeated a number of times. Some idea was thus gained of the percentage of bacteria that remained in the sand after the original treatment. These figures ranged from 10 to 30% with an average of 20%. Consequently, all figures on bacterial populations which follow are nothing more than an approximation of from 70 to 90% of the number of aerobic, saprophytic bacteria which formed macroscopic colonies at room temperature after incubation from five to seven days on the medium employed, which were present in the sand at the time of sampling. No estimation can be given as to what portion of total population of bacteria in Beaufort sand beaches was measured by this method. The direct microscopic method would have to be used to do this and when it is used, non-living cells and those which will not divide are usually counted. Knaysi (1935) describes a method for distinguishing between dead and living bacteria by the use of neutral red.

Many bacteria were still clinging to each sand grain even after it had been shaken in six or eight different aliquots of water. Each grain became surrounded by abundant growth when poured into agar. It is probable that these were certain species of bacteria which were most tenacious in their attachment and that a very few of them were dislodged. Three species of this type were described by ZoBell & Allen (1935).

Media Used

Several media were tried under identical conditions to determine which would give highest counts. The marine agar used by Reuszer (1933) (1 gr. peptone, 1 gr. glucose, 0.05 gr. K_2HPO_4, 15 gr. agar, 1 liter sea water) did not yield as high a count as ZoBell and Feltham's (1934) agar (5 gr. peptone, 2 gr. beef extract, 0.5 gr. KNO_3, 15 gr. agar, 1 liter sea water). Highest counts were obtained by adding five grams glucose per liter to the medium used by ZoBell and Feltham and this was therefore used in routine counts. Agar-digesting bacteria were counted on Stanier's (1941) medium (5 gr. peptone, 2 gr. K_2HPO_4, 15 gr. agar, 1 liter sea water). Isolations were sometimes made from a modified Chodat-Grintzesco medium (Fred & Peterson 1925) made up in sea water, and from plain sea water agar to which 1 gr. $CaNO_3$ and 0.2 gr. K_2HPO_4 were added. Chodat-Grintzesco medium was made up primarily for cultivating marine diatoms, many species of which thrived upon it.

Results of Counts

The average count for all sand samples taken in the intertidal zone at all stations during the summer of 1941 was 200,000 per gram. This is a result of pouring 256 plates. Most samples were taken while tides were low. Allowances were not made for moisture content of samples. Those taken at mid-tide usually had their "field capacity" whereas those from the low tide mark were saturated with water. High tide samples were usually dry.

The high tide average for all samples was 486,000 per gram; mid-tide, 110,000 per gram; low tide, 34,000 per gram. Figures are given to the nearest 1,000 of the actual average.

The lowest count of any single gram of sand measured was 5,000 per gram in a low tide sample taken at Station V on July 28. The highest was 1,250,000 for a high tide sample taken at Station V, August 1. Highest count of any low tide sample was 190,000, taken from inner beach, Shackleford Banks, July 3. Lowest count of any high tide sample was 33,000 from Station V, August 12. Lowest and highest records from mid-tide samples taken were 10,000 and 700,000 respectively. The former sample came from the "crest" at Station VI on July 29, regarded as mid-tide because it was covered with about one foot of water at high tide. The latter came from inner beach, Shackleford Banks, July 3.

During the early part of the work, the "attachment count" method was used in an attempt to check on relative counts given by plating. This was unsuccessful, as might be expected, because of the great

variation in water content of intertidal sand at low, mid-, and high tide marks.

Numbers of Agar-Digesters

Preliminary counts of agar-digesters ran from an average of 200 per gram of sand to 15,000. As in other counts, highest figures came from high tide samples. Instead of relying upon depressions in agar, made more readily by surface colonies than by subsurface colonies, each plate was flooded with a solution of I_2KI after incubating for about seven days. Each discrete clear area was counted as one agar-digesting colony. Counting was not possible on some plates because there were so many agar-digesters present that the entire agar contents of the plates had been rendered unstainable. Visual examination of such plates would not have given accurate counts.

Spreading Colonies

At least two species of bacteria common in Beaufort sand beaches are characterized by a tendency to spread rapidly on agar. One spreads much more rapidly than the other and records were kept of numbers of these appearing on all plates. The remarkable spreading ability of these colonies on agar is the result of extremely rapid motility or streaming of the organisms making up a colony. Examination under the 4 mm. objective of a microscope reveals a maze of streaming and flowing that is constantly changing, especially near the margins of the colony. Cells at the very margin are usually motionless and are being pushed outward by those inside. Continued observation over a period of five or ten minutes will enable the observer to see the colony spread. Cells in any given stream all seem to be oriented longitudinally with the direction of flow, and movement of the stream continues until it is interrupted or broken up by other streams. Examination of cells in a hanging drop does not reveal the active motility which might be expected after viewing the colony. Many cells are actively motile but many others are motionless.

The two species are similar morphologically with respect to both individuals and colonies, except that colonies of one species spread more rapidly, often forming an unbroken film of uniform thickness over the entire surface of a Petri dish in less than 24 hours. Physiologically they are similar in many respects but differ sufficiently to justify classification as different species. Apparently they belong to genus Achromobacter. Neither species appears to be described in Bergey's Manual.

Although of frequent occurrence in low and mid-tide samples, neither species was observed from any high tide samples. Calculations of numbers per gram show an average of 1,400 at low tide and 750 at mid-tide. Apparently they are very susceptible to desiccation and are obligate marine bacteria, as they failed to grow on any agar medium made up with freshwater. Both grew in freshwater gelatin and litmus milk, however.

"Freshwater" Bacteria in Ocean Beaches

Occasional plates were poured of ordinary freshwater nutrient agar in order to determine approximate numbers of bacteria in the beach which would develop on this medium. An average of 30 plates from low, mid-, and high tide marks of the intertidal zone gave 2,000 per gram. Average at high tide was 4,000; at mid-tide, 400; at low tide, 1,800. These anomolous-appearing results may be related to the inadequate number of plates poured, or to unknown factors controlling the number of bacteria in various parts of the beach which will develop on freshwater agar.

ARE THERE SPECIFIC MARINE BACTERIA?

Even the most skeptical must hesitate to answer this oft-discussed question in the negative. Many species of bacteria have been described which have been isolated only from the ocean and which do not grow unless the salt concentration is within a certain range, the lower end of which is well above that of fresh water. These, it seems, must be regarded as specific marine bacteria until they have been shown to occur naturally in some other habitat.

Stanier (1941) studied seven species of agar-digesters which he apparently regards as marine bacteria. He points out the unreliability of temperature and salinity tolerations and suggests physiologically similar groups of bacteria from soil and the sea be studied and compared, including various autotrophs, nitrogen-fixers and aerobic cellulose decomposers, in an effort to answer the question.

Beneeke & Keutner (1903) were unable to find any difference between strains of *Azotobacter chroococcum* and *Clostridium pasteurianum* which they isolated from ocean bottom and typical soil strains.

Burke (1934) states that many freshwater bacteria can carry on their activities in salt concentrations equivalent to or greater than that occurring in the sea, although the death rate of freshwater species entering the sea is undoubtedly high. He showed that cells of young cultures are more susceptible to salinity changes than older cultures. Greatest resistance is reached in 24 to 48 hour cultures. He also pointed out that changes in salinity often affect other characteristics of a species. Thus bacteria from the sea which develop on freshwater media may include cells which happened to be in a stage of growth most tolerant to salinity changes.

POPULATION CHANGES IN STORED BEACH SAND

Bacterial populations begin an immediate and rapid rise when a sample of sea water is stored or kept in a container. Oxidation of part of the organic matter in solution and in suspension makes such multiplication possible (Waksman & Carey 1933). This increase of bacteria may be from 1,000 to 10,000 times the original number at the end of 24 hours, depending upon the ratio of solid surface to volume of stored water and other factors (ZoBell & Anderson 1936). A peak is usually reached in two

or three days, depending mainly upon temperature, and then there is a relatively gradual decline.

Preliminary observations were made on the behavior of bacterial populations of stored beach sand in an effort to compare it with behavior reported for stored water samples. Of four two-ounce jars filled from various locations on the beach, three reached their peak of population on the eighth day when kept at room temperature (25 to 30° C.). The fourth, filled with dry sand from high tide mark, had doubled in population on the second day and then began a decline in which the population was half the original number at the end of a week. The other three samples were composed of wet sand, two taken from mid-tide mark and one from low tide mark. All were taken while the tide was low. These three increased gradually through the third day and then on the fourth day population of all three declined suddenly to well below half the original number. This was followed by a rapid rise to a peak on the eighth day. Addition of sterile sea water to a half tide sample so that the sand was saturated but contained no water at the surface resulted in a much higher peak. The maximum was even higher when nitrates and phosphates were included with sterile water. All stored samples declined to about the original number during the third week. Daily duplicate samples were plated during the first two weeks.

Incomplete as these results are, they show that there is a rise in population of bacteria in stored beach sand similar to that in stored water samples but that it differs in several respects from the behavior of the population in stored water. In sand, both rise and decline seem to be slower and maximum bacterial population much lower. In samples to which sterile water, nitrates, and phosphates had been added, the maximum was greatest, but it was only 20 times the original number. A low tide sample from which water was allowed to drain until only "field capacity" remained had increased but six times its original population when the peak was reached on the eighth day.

Added difficulty and sources of error make plate counts of sand samples less reliable than those from water and consequently results of these preliminary observations may contain serious inaccuracies. Additional work should be done with stored sand and bottom samples not only to study behavior of bacterial populations in them, but also as a possible source of additional information on stored sea water and influencing factors. It would be interesting to know what effects the addition of phosphates and nitrates, both separately and together, would have. A study should be made of the amount of organic matter present before and after storage, of the effects of particle size, moisture content, and other factors.

PURE CULTURES

In addition to cultures already discussed, the following were identified from the intertidal zone at Station IV and V: *Sarcina subflava* Ravenel, *Micro-coccus halophilus* Bergey et al., and *Micrococcus varians* Migula.

Difficulty was encountered in attempting to identify many other cultures. One interesting species, to be studied in detail, produced abundant gas from, or in the presence of, nitrates.

Two cultures of the genus Micrococcus could not be identified to species. Both were opaque-white, liquefied gelatin, and produced nitrites from nitrates, but were sufficiently different in other respects to be distinctly different species.

These and other cultures will be investigated in detail and possibly described.

SUMMARY

Large quantities of organic matter are decomposed and mineralized on Beaufort beaches and decomposition products returned to the sea. Apparently bacterial activity goes on at a greater rate in the intertidal zone when tides are out. It is very likely that the same bacteriological processes take place on beaches as in ocean water and bottom such as nitrogen fixation, nitrification, reduction of nitrates to nitrites and of nitrites to ammonia, and denitrification.

An average of over 250 poured plates from all parts of the intertidal zone during June, July, and August, 1941, gave 200,000 bacteria per gram of sand. This is probably from 70 to 90% of the total number of aerobes which would form macroscopic colonies on the medium employed at room temperature within seven days. Anaerobes and other special groups are not included. The numbers ranged from 5,000 to 1,250,000 in the grams of sand used as samples.

Numbers of agar-digesters per gram ranged from 200 to 15,000 in preliminary counts. Both agar-digesters and chitin-digesters are discussed and the literature briefly reviewed in so far as it might apply to sand beaches. These bacteria release much otherwise unavailable organic material which other bacteria utilize.

Numbers of bacteria in Beaufort beaches which will develop on ordinary, freshwater nutrient agar averaged 2,000 per gram. The question of specific marine bacteria is reviewed and discussed briefly.

The rise in population of bacteria in sand samples stored in jars was observed in a preliminary way. Populations increased 20-fold, and reached a peak on the eighth day.

A number of pure cultures were studied and identified where possible.

ALGAE OF SAND BEACHES

INTRODUCTION

Algae concerned in the ecology of sand beaches may be divided into two groups: (1) microscopic, one-celled species which grow naturally on or in beach sand; and (2) macroscopic, many-celled species which grow attached or are pelagic and later wash ashore. As previously mentioned, macroscopic species which wash ashore are further divided into two groups by weather conditions: (1) brown algae of

genus Sargassum composed mainly of two strictly pelagic species and others which are attached at first but drift in with those which are pelagic, and (2) red, green, and brown algae which grow attached in shallow water near the beach. Macroscopic algae constitute a significant source of organic matter on beaches.

MACROSCOPIC ALGAE

Sargassum

Several times during the summer of 1941 storms brought Sargassum to the beach in quantity. Particularly on July 18, 19, and 20 outer beaches were littered with it. While tides were low, Sargassum was distributed along the beach in a band about 100 feet wide in addition to a heavy accumulation at the drift line left by the previous high tide. Six species found were identified as *S. polyceratium* Montagne *sensu lato*, *S. fluitans* Borgesen, *S. natans* (L.) Meyen, *S. pteropleuron* Grunow, *S. filipendula* Agardh., and *S. filipendula var. montagnei* (Bailey) Collins and Hervey.

On July 18, the first day of strong winds (which began the night of July 17-18), over 95% of all Sargassum on the beach was *S. natans*. This material was so covered with an epiphytic, bluegreen alga, *Dichothrix penicillata* Zanardini ex Bornet and Flahault, that it looked as though it had been spattered with tar. The epiphyte is dark olive-green in color. On July 20, a totally different Sargassum flora was washing in although the quantity was undiminished. About 90% was *S. polyceratium* and 5% an unusual form of *S. pteropleuron*. Other species were *S. natans*, *S. fluitans*, two varieties of *S. filipendula*, and occasional typical *S. pteropleuron*.

S. natans and *S. fluitans* are strictly pelagic species, not having been reported growing attached. Neither has been known to fruit. *S. filipendula* (including *var. montagnei*) grows attached in the harbor and on rocks at Beaufort. The other three species were found fruiting. They drifted in with pelagic species but probably grew attached on coral reefs paralleling the Gulf Stream either off-shore from Beaufort or farther south. Hoyt (1918) found but two species at Beaufort, *S. filipendula* (including *var. montagnei*) and *S. natans*.

Possibly *S. natans*, which washed ashore on the first day of high winds, had been floating in the Gulf Stream. Continued rough seas dislodged attached species which washed ashore later, after most of the *S. natans* had already been cast up to the drift line.

Local Attached Algae

On July 21, Sargassum had almost ceased washing in but great quantities of algae which grew attached in the vicinity of Beaufort appeared on the beach and in the surf. The strong winds had been replaced by light breezes. It was strange that these local, attached species had not appeared among the Sargassum while the winds were high and seas heavy.

Species collected on outer Fort Macon beach (Stations IV and V) during low tide, July 21, were as follows. Rhodophyceae: *Polysiphonia havanensis* Montagne, *Dasya pedicellata* Agardh., *Champia parvula* (Agardh.) Harvey, *Hypnea musciformis* (Wulfen) Lamouroux, *Gracilaria confervoides* (L.) Greville, *G. multipartita* (Clemente) J. Agardh. *sensu* Hoyt (1918), *Meristotheca duchassaingii* Agardh., *Nitophyllum medium* Hoyt; Chlorophyceae: *Ulva lactuca* L., *Codium decorticatum* (Woodward) M. A. Howe; Phaeophyceae: *Dictyota dichotoma* (Hudson) Lamouroux, *Zonaria flava* (Clemente) Agardh.

In addition, the following species were found at other times during July and August on the ocean beach. Rhodophyceae: *Rhodymenia palmetta* (Esper) Greville, *Gelidium crinale* (Turner) J. Agardh.; Phaeophyceae: *Padina vickersiae* Hoyt. Species which were taken repeatedly in a dredge off the outer beach during July and August include the following: Rhodophyceae: *Gracilaria confervoides, Hypnea musciformis, Rhodymenia palmetta, Nitophyllum medium, Gracilaria multipartita;* Chlorophyceae: *Ulva lactuca, Codium decorticatum;* Phaeophyceae: *Dictyota dichotoma, Zonaria flava.*

The following algae occurred epiphytically upon Sargassum: *Spyridia filamentosa* (Wulfen) Harvey, *Dasya rigidula* (Keutzing) Ardissone, *Polysiphonia harveyi* Bailey, *Achrochaetium* sp. and *Callithamnion* sp.

Ectocarpus mitchellae Harvey was found attached to the spires of three live specimens of *Olivella mutica* and on one living *Donax variabilis*.

MICROSCOPIC ALGAE

Four phyla (Divisions) of the plant kingdom are well represented in marine sand beaches by species indigenous to this habitat. Chrysophyta (Bacillariophyceae) are apparently most common, but it is likely that Chlorophyta, Pyrrophyta, and Cyanophyta are much more common and more important than is generally believed. These one-celled plants are rarely seen with the unaided eye and very little work has been done to determine their numbers and significance in beach sand. Diatoms have received more attention than other one-celled types. Phifer (1929) made a quantitative and qualitative study of diatoms living naturally in the intertidal zone of Argyle Lagoon near Friday Harbor, Washington.

The abundance of one-celled plants living in beach sand cannot be estimated with the unaided eye. Even a dissecting microscope is inadequate to judge such a population. Many of the bluegreen and green algal cells are less than 10 microns in their longest axis or in diameter. Some species of bluegreen algae average but 3 microns in diameter. On Beaufort beaches, only two species of diatoms were detected in the field and of the other phyla only Pyrrophyta (Peridinium) were sufficiently concentrated to be visible. *Hantschia virgata* (Roper) Grun., a large diatom essentially rectangular in valve view, often formed large, irregular, greenish-brown patches on hard, fine sand of tidal flats at Station VI (Fig. 1) during July and August. It also oc-

curred on beaches in Beaufort harbor and along inlets. Attempts to grow this species in culture were unsuccessful. *Nitzschia closterium* W. Sm. was observed several times inhabiting the jelly of egg masses of a marine worm, *Clymenella torquata* Leidy, in such numbers as to impart a greenish-brown color to the egg case. Clymenella is common on tidal sand flats at Beaufort. Miss Jo Bridgman first called our attention to this phenomenon. It appeared that the diatoms were digesting the material in which the worm eggs were embedded. Several times during July and August a species of Peridinium was so thick in tidal pools on the ocean beach near Station IV that the water was greenish in color, especially near the margins of the pool. Thus, if the abundance of one-celled plants was judged solely on the basis of visible accumulations or even by low-power microscopic examination of sand, they would not appear to be very important in Beaufort beaches.

Only by application of bacteriological methods can a reasonably accurate survey of the one-celled algal flora of beach sand be carried on. A modification of both the direct microscopic method of determining bacterial numbers and of the plating method can be used. Since the latter procedure would take into account only those species which can be cultivated artificially, the direct microscopic method would serve as a valuable supplement. Identification of species would be less difficult if the organisms were in culture, because of the unlimited supply and possibilities of determining variation, even though variability be of greater latitude in culture than in the natural habitat. Probably the majority of one-celled species inhabiting sand are amenable to culture because of a tolerance they must have to wide and rapid environmental changes in order to live in such a habitat. Besides making it possible to give a reasonable estimate of numbers and to determine species inhabiting sand (some of which may be undescribed), it is but a step from an ordinary culture to a perfectly bacteria-free culture by means of which a knowledge of the physiology of the species involved may be gained.

One-celled algae from the intertidal zone were easily grown on a modified Chodat-Grintzesco agar (Fred & Peterson 1925) made up in sea water. Since this medium was originally designed for fresh-water species, probably some of the constituents are superfluous when sea water is used. A few grams of moist sand were placed in sterile water, as previously described, and this mixture poured rapidly back and forth between two beakers until diatoms and other unicellular algae were brought into suspension. Some of this suspension was spread on cool, hardened agar in Petri dishes. For quantitative determinations a definite amount of sand and dilution water must be used as well as a known amount of inoculum. The incubation period must be long, at least a month, and in localities where humidity is not high, some expedient must be employed to reduce water loss from the agar substrate. In general, smaller species of diatoms are more readily cultivated than larger species.

Cultural technique indicated that one of the most common diatoms in Beaufort beaches is *Nitzschia closterium* W. Sm. It appeared on almost every plate inoculated and its active motility and long, slender shape seem to adapt it to living in loose, moist sand. Other genera which appeared in culture were Melosira, Coconeis, Biddulphia, Navicula, and Pleurosigma.

Bluegreen algae which developed in culture were single, non-colonial cells which either lacked a sheath or possessed a very thin one. Both rod-shaped and coccus cells were represented most of which measured from 3 to 6 microns. Although most colonies were bluegreen in color, one appeared that was yellow-brown and another was rose-red. No trace of the red color was visible in individual cells of the latter.

Green algae were mostly simple, non-colonial coccus cells of less than 10 microns in diameter. Euglena appeared on one plate in agar which had been liquefied by bacteria. Attempts to transfer were unsuccessful. Efforts to grow in culture the species of Peridinium which appeared in tidal pools were also unsuccessful. Only one medium was tried, however.

Although plankton algae are retained to a certain extent by sand in the intertidal zone when tides are in, it is not likely that plankton species would be confused with sand-inhabiting species in culture. Those indigenous to sand would be more numerous and more likely to develop. The two flora could be compared by inoculating agar plates from plankton tow and from sand washings at the same time. It is possible that some species, especially tiny bluegreen cells, occur naturally in both places.

SUMMARY

Algae of sand beaches may be divided into two groups: (1) macroscopic, many-celled species which wash ashore; and (2) microscopic, one-celled species which grow naturally in sand.

Many-celled algae which wash ashore may be divided into two groups: (1) brown algae of the genus Sargassum, some species of which are always pelagic, others of which are attached first but become pelagic later; (2) red, green, and brown algae which grow attached in the vicinity of Beaufort. During storms the two groups are usually washed ashore at different times, the Sargassum appearing first, the local flora later. Five species of Sargassum were collected on July 20 and identified. About 20 species of local attached algae were found on the beach during the summer.

One-celled species include representatives of the phyla Chrysophyta (diatoms), Chlorophyta (green), Pyrrophyta (Peridinians), and Cyanophyta (bluegreen). Application of bacteriological methods, such as culture on agar, show these one-celled species to be widely distributed in beach sand and probably much more significant in the economy of the beach than previously supposed. Only rarely are they numerous or concentrated enough to be visible to the

unaided eye. Most green and bluegreen algae living in sand are individual rather than colonial, do not have a well-developed sheath, and are very small, usually from 3 to 10 microns. They are easy to grow on agar. *Nitzschia closterium* W. Sm. and *Hantschia virgata* (Roper) Grun. are two of the most common sand-dwelling diatoms at Beaufort in summer. *N. closterium* is easily cultured.

Thanks are due Mr. Paul Conger of the Smithsonian Institution for identification of diatoms and Mr. A. E. Parr, Director of the Peabody Museum of Natural History, Yale University, for identification of Sargassum.

GENERAL DISCUSSION

Sand beaches at Beaufort are in the temperate region where they experience marked seasonal changes, but they are never subject to the action of ice. Though many plants and animals are less active in winter, few appear actually to hibernate. Some larger animals (blue crabs) retreat to deeper water and may remain inactive on suitable bottoms in winter, but smaller animals (Donax, Emerita, Haustorius) are to be found in the wave-swept intertidal zone at all seasons. The Gulf Stream is only about 25 miles offshore; so strong winds often bring in plants and animals that are characteristic of regions farther south.

Beaufort sand beaches do not contain much humus and lime, compared to some beaches in estuaries and many tropical "coral strands." As in all sand beaches oxygen decreases rapidly below the surface, so that below a few centimeters there is none. However, more oxygen is present when a tide has fallen than after it rises, as air is sucked in between particles when the ocean recedes, and oxygen in sand is soon used up when tides cover over beaches. The beaches studied by the writers were all bordered by sea water, so that variations in salinity and pH were insignificant.

Most of the characteristic sand beach plants and animals live near the surface, but bacteria and nematodes are quite numerous at depths of 15-20 cm. in sand (Table 4). Some of the former are doubtless anaerobic. Some worms and crustaceans live in burrows that reach depths of a meter or more. These have special organs adapted to create currents for respiration.

Although a sand beach appears to be barren, it teems with life. In each gram of intertidal beach sand at Beaufort there are perhaps 500,000 bacteria, as well as numerous minute diatoms and other algae. In an average liter of beach sand there are microscopic animals about as follows (Table 3):

Fort Macon, outside: 260 nematodes, 180 copepods, 75 Asterigerina, and others.

Forst Macon, inside: 350 nematodes, 140 copepods, 50 Asterigerina, and others.

Bird and Sheepshead Shoals: 480 nematodes, 630 copepods, 100 ostracods, 40 Asterigerina, and others.

Among typical larger animals, as judged by sieve catches (Table 5), there will be in each liter on Bird and Sheepshead Shoals Haustorius as follows: high tide mark, 17; half tide, 21; low tide mark, 7; 0.5 m. below low tide mark, 1.5; at a depth of 3.5 m., 0.5. Donax per liter on Fort Macon beach inside will be present in about the following numbers: high tide mark, 0.01; half tide, 8; low tide mark, 24; 0.5 m. below low tide mark, 0.03. On Bird and Sheepshead Shoals, which are inundated at high tide, there are more Donax per liter (0.6) at high tide mark than at any level below. In addition to such typical beach animals here cited as examples, there are of course many others that occur in smaller numbers.

With every ebb and flow of tides conditions on a sand beach change. Bacteria multiply more rapidly when beaches are left exposed at low tide. Then birds, ghost crabs, and beach amphipods come to hunt over beaches. When a tide rises fishes, crabs, and other animals come in from the sea. Waves and currents continually move sand grains and, if violent, may change the whole contour of a beach in a few hours. Tidal rhythms by alternately exposing beaches to desiccation in the atmosphere and inundation by sea water have played a role in the evolution of land animals from marine ancestors (Pearse 1936a).

In general typical beach animals show more or less tendency to segregation into definite zones. Pennak (1941) has shown that seven species of burrowing copepods are definitely arranged, each species at different level, on beaches at Woods Hole, Mass. Slope and degree of inundation also influence the number and character of the biota of a sand beach. At Beaufort Donax occurs in greatest numbers on the steep slopes on the beaches inside Fort Macon (Table 5), but Haustorius was most abundant on the flats of Bird and Sheepshead Shoals that were covered by the sea at every high tide (Table 5). At Beaufort some animals move back and forth more or less with rising and falling tides (Emerita, Donax, Ocypode, Callinectes, Menidia, etc.), others remain at or near low tide mark (Mellita, Terebra, Ogyris, Lepidopa; Table 5) where they get the benefits of currents and waves but are not exposed to desiccation, and some are usually found at levels below ordinary wave and tidal influences (Renilla).

Plants and animals on marine sand beaches live in a changeful environment—subjected to shifting sand, beating waves, desiccation, lack of oxygen, attacks by terrestrial and marine enemies, etc. Many of them show striking adaptations. Some of the epifauna are protectively colored, but most of the subterranean animals lack pigment. Microscopic nematodes, copepods, and other animals creep about between sand granules. Burrowing crustaceans (Figs. 10-14) have setose appendages modified for digging and show a tendency to have small eyes. Those that remain near the surface have long antennae and more or less robust bodies; those that live in deep burrows have slender bodies (except terrestrial types, such as Ocypode) and short antennae. Burrowing clams that

remain near the surface of sand have heavy shells and short siphons, those that burrow deep have more fragile shells and tend to have longer siphons (Fig. 9). Sand beach snails are of two types (Fig. 4): (1) those that have a broad, flat, slimy foot move with ease directly through sand and show a tendency to have reduced shell; and (2) those that burrow by plunging a narrow foot into the sand below their body, expanding the end, and pulling themselves into the sand. Psammobionts that live at or near the surface have little difficulty in breathing, but those that live in burrows have various means of creating currents. Animals that are buried in sand may have difficulty in finding mates. Wharton (p. 163) believes that Emerita swims about in the surf while mating and Lunz (1937) suggests that Callianassa leaves its burrows and looks for mates above the sand.

Plants that live on sand beaches are all small in size. Bacteria, minute diatoms, and other algae move about among sand granules and at times form coatings over sandy surfaces. They are one basis for the "food chains" that are inherent in sand beaches. Several types of animals are known to feed on such minute plants—various protozoans and worms, copepods (Wilson 1935), Ophiurans, sea cucumbers (Grave 1902) Callianassa (Mac Ginitie 1934), etc.

There are extensive food resources in marine sand beaches. Organic materials are added in the feces of birds and as stranded plant or animal remains. Humm and previous workers have shown that sand-dwelling bacteria include nitrogen-fixers and digesters of agar, gelatin, cellulose, starch, chitin, and other more or less indigestible compounds. Saprophytic bacteria release ammonia that is oxidized by autotrophic types. Denitrifying bacteria are rare, and little nitrate is lost on sand beaches. Among beach animals there are those that feed on plankton by siphoning water into their bodies (clams) and catching the contained organisms on slime threads; some that sweep delicate tentacles over bottoms and wipe up small organisms (Thyone); some that spin slime thread snares that catch small plants and animals and are then devoured (sipunculids); some that fish with setose nets and thus catch organisms from the water (Emerita, Pinnixa), some that sort over sand and with setose appendages brush out the microscopic organisms (Callianassa); and others that swallow great quantities of sand and digest the contained food substances (Arenicola, Balanoglossus). Many of these specialized animals are devoured by predators (plovers, sandpipers, killifish, crabs, snails, etc.). A sand beach is an incubator and digestive system that continually produces foods for the ocean.

A sand beach is not a barren, desolate place that is without interest to man. It has scientific and economic value. We have only scratched the surface of many problems that our very general survey suggests. Sand beaches are continually producing resources that are gradually built up through food chains, which may extend from bacteria to whales, into products that are of economic value.

SUMMARY

1. Sand beaches at Beaufort, N. C., have been studied throughout two summers (1939, 1941) and at intervals at other seasons during three years.

2. In order to estimate populations, routine collections were made by using spades, rakes, salve boxes, sieves, diving hood, trawl, seine, and dredge. Seven stations were selected for detailed study; these included various types of sand beaches—shoals in sounds, abrupt slopes, flats, strands along the open sea, etc. At intervals collections were made at other localities.

3. Observations were made on temperature, salinity, ionization, oxygen, particle size (Table 1), humus, and calcium. Beaches contained little calcium (Table 2) and humus; oxygen was usually absent at depths of 5-10 cm. in sand (Table 3); air was usually cooler than water and sand in summer and warmer in winter; salinities were all near those in the open ocean.

4. In sand beaches abundant microscopic animals were nematodes, copepods, foraminiferans, polychaetes, ostracods, amphipods, and flatworms (Table 4). Larger common intertidal animals were Haustorius, Emerita, Donax, polychaetes, Chiridotea, etc. Common shore fishes were Menidia and Fundulus; with them were Callinectes and other crustaceans (Table 6). Just below low tide mark such animals as Mellita and Terebra were common.

5. Beach animals are arranged more or less in zones. Typical examples of those that are most abundant at various levels are as follows: above high tide mark, Ocypode, Talorchestia; high tide mark, bacteria; between tides, Haustorius; low tide mark, Emerita, Donax; 0.5 m. below low tide mark, Terebra, Mellita, Arenaeus, Lepidopa; 10-15 m. deep, Renilla.

6. Burrowing crustaceans are mostly of three kinds: (1) minute, slender forms that creep about between sand granules (Copepods), (2) stocky forms that are expert burrowers with long antennae and remain near the surface, (3) slender forms that live in deep (1 m.) burrows and have special pumping organs for creating currents (Fig. 10). Emerita has been described in some detail as an example of a sand beach crustacean.

7. Burrowing molluscs have either a wide, slimy foot and small shell and crawl with ease directly through sand, or have a slender foot that can expand at the end and give enough anchorage so that the animal can pull itself downward (Figs. 4, 8).

8. Sand beach animals usually lack colors and patterns, but some are colored like sand (Ocypode) and a few are speckled (Ovalipes, flounders). Most crustaceans have small eyes.

9. Sand beaches contain enormous food resources; they are great digestive and incubating systems. Bacteria break down organic remains and continually supply the ocean with phosphates, nitrogen compounds, and other valuable materials. There are various types that can fix nitrogen and digest agar,

cellulose, chitin, and other rather refractory organic substances. Bacteria, minute diatoms and other algae are eaten by protozoans, worms, echinoderms, crustaceans, molluscs, etc.; these in turn furnish food for fishes, birds, and other large animals.

10. Microscopic beach organisms multiply very rapidly. Bacteria and protozoans may increase enormously in number in a few hours. Many small beach animals (Emerita, Donax) are annuals, but larger animals (Callinectes) live several years. Reproduction is most active among beach animals during summer, but a few are breeding at all seasons.

11. Sand beaches are not barren wastes, as they appear at first glance, but are swarming with life, and continually digest and furnish food to plants and animals.

12. An appendix that gives the names of animals found on Beaufort beaches follows.

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APPENDIX I

LIST OF ANIMALS FOUND ON AND IN SAND BEACHES AT BEAUFORT, N. C.

This list of course does not pretend to give a complete account of the fauna of the Beaufort region, or even that of sand beaches, but only includes species that were encountered.

Protozoa
Foraminifera

Asterigerina carinata d'Orbigny was common in salve box samples on all beaches investigated. It was most abundant along the open sea and least on the flats along Bird Shoal (Table 4).

Quinquiloculina semiluna (L.), was taken several times in salve box samples from mid- and low-tide levels; four times on the beach outside Fort Macon, four times on Bird Shoal, and once on Shackelford Bank.

Mastigophora, Ciliata

Small flagellates and various types of ciliates were observed at times in salve box samples from all beaches studied. These were not counted accurately or identified. Ciliates were sometimes quite common, perhaps when considerable organic materials and bacteria were present.

Metazoa
Parazoa
Porifera

No sponges were found living on or in sand beaches, but during storms they were at times washed up. In 1941 *Microciona prolifera* Verrill was seined outside Fort Macon (Station 4), June 17, and taken in a dredge along the margin of Bird Shoal, July 16; *Lissodendoryx carolinensis* Wilson was twice taken in the ocean outside Fort Macon, July 15, 16.

Enterozoa
Coelenterata
Cnidaria
Hydrozoa
Hydractiniidae

Hydractinia echinata Fleming was common on the shells of *Pagurus longicarpus* and *P. pollicaris*.

Siphonophora
Physaliidae

Physalia pelagica Bosc was at times cast up by storms on the beaches at Stations IV, V, VI, and VII (Fig. 1). During July, 1941, it was found twice (1, 3) on Sheepshead Shoal and once (2) on the beach outside Fort Macon (V).

Scyphozoa
Cubomedusida
Charybdeidae

Chiropsalmus quadrimanus Agassiz was taken twice in dredge hauls at a depth of 3 m. off Station V on July 16, 1941, and seined at Station II, July 7, 1939.

Rhizostomida

Stomolophus meleagris Agassiz was at times abundant in the sea outside Beaufort Inlet and was left stranded on the beach at Stations IV and V; as on May 31, 1941.

Anthozoa
Gorgonacea
Gorganiidae

Leptogorgia vingulata was often dredged in the deeper parts of sounds and off the beaches.

Pennatulacea
Renillidae

Renilla reniformis (Pallas) was often dredged offshore outside Beaufort Inlet and was not uncommon inside Shackleford Bank.

Actinaria
Edwardsiae

Edwardsiella lineata Verrill was taken August 9, 1939 on the border of Guthrie Shoal, at the water's edge.

Cerianthidae

Cerianthus americanus Verrill was taken just below low tide mark on Sheepshead Shoal, July 25 and August 5, 1939.

Paractidae

Paractis rapiformis (Lesson) was found near low water mark at Stations IV and V on June 17, July 18, 21, 1941.

Sagartiidae

Adamsia tricolor Lesson often occurred on the shells of *Pagurus pollicaris* from moderate depths (3-6 m.) on sand bottoms.

Madreporia
Astraeidae

Astrangia danae Agassiz was at times dredged from sandy bottoms, where it was attached to shells or other solid objects. This coral has a wide range, from piles on the piers in Beaufort Harbor to deep waters offshore.

Acnidaria (Ctenophora)
Tentaculata
Lobata
Mnemiidae

Mnemiopsis leidyi A. Agassiz varied greatly in different seasons. In 1939 it was collected July 12, 15, 17, 29, and August 2 at Stations I, IV, V, and VII. During 1941 it was not seen after early spring.

Platyhelmintha
Turbellaria

Small flatworms were often observed in salve box collections and were sometimes shown to W. A. Kepner, Margaret A. Stirewalt, or Frederick Ferguson, all of the University of Virginia, who classified them.

Acoela, Rhabdocoela, Alloeocoela

During July and August, 1939 acoels occurred in salve box samples from sand beaches (Stations I, II, IV, VII). Rhabdocoels also appeared often in salve box samples from Sheepshead Shoal during July and August, 1939, and were in those from Fort Macon beaches once on June 19 and once on July 24. In the summer of 1941 *Archiloa wilsoni* Stirewalt, Kepner, & Ferguson was present in samples from Bird Shoal and beaches outside Fort Macon, in June and July. Another rhabdocoel, *Trigonostomum prytherichi* Kepner, Ferguson, & Stirewalt, was in algae washed up along Fort Macon Beach, August 3, 1941. On that date also Miss Stire-

walt found several alloeocoels, which included representatives of the genera Polycystis, Cylindrostoma, Plagiostomum, etc.; and a triclad.

Tricladida

Bdelloura candida (Girard) was common on *Limulus polyphemus* on the flats along Bird and Sheepshead Shoals.

Nemertea

Nemerteans were quite common in sieve catches. They were more often encountered on shoals in sounds and on beaches inside Fort Macon than on those along the open sea. *Cerebratulus lacteus* (Leidy) and *Lineus* sp. were among species observed.

Nematoda

Nematodes were very common in salve box samples (Table 4). All collections were sent to Dr. B. G. Chitwood, who has kindly identified them. Nematodes appeared to flourish at greater depths in sand, where oxygen was scanty or absent, than other microscopic animals. Dr. Chitwood's determinations of over sixty species of nematode worms were as follows:

Manhysteridae

Xyala striata Cobb was common at half tide, low tide, and below on Sheepshead Shoal, down to depths of 10 cm. in sand. It was also collected at times on the beaches around Fort Macon.

Halamonchus macramphidium Chitwood was taken once between tides on Sheepshead Shoal, and once in Lighthouse Bay, Cape Lookout.

Cobbia sp. was found in sand from tide pools on Sheepshead Shoal, and at Cape Lookout and on the beach outside Fort Macon.

Theristus sp. Five or six species were present, often several in a collection.

Paramanhystera sp. was collected from Sheepshead Shoal and the beaches about Fort Macon.

Steineria sp. was taken several times on Sheepshead Shoal, once at Lighthouse Bay, Cape Lookout, and on the beach outside Fort Macon.

Axonolaimidae

Axonolaimus sp. was present in sand from tide pools outside Fort Macon.

Ascolaimus elongatus? (Butchli) was collected from sand taken at a depth of 6.5 m. outside Fort Macon.

Cyartonema flexile? Cobb; Sheepshead Shoal, between tides.

Odontophora angustilaima Filipjev; Bird Shoal flats; Fort Macon outside, 6.5 m.; Lighthouse Bay, Cape Lookout.

Comesomatidae

Laimella hexasetosa Chitwood; several times on Sheepshead Shoal between tides and below tide pools; Fort Macon beach inside; Guthrie Shoal.

Laemella sp.; Fort Macon beach, inside.

Laemella quadrisetosa Chitwood; Lighthouse Bay, Cape Lookout.

Comesoma sp.; Sheepshead Shoal, intertidal, 15 cm. deep in sand.

Sabatieria celtica Southern; Sheepshead Shoal, intertidal, 15 cm. deep in sand. Two other species of Sabatieria were also found on Sheepshead Shoal, intertidal.

Camacolaimidae

Camacolaimus prytherchi Chitwood; Fort Macon beach inside; intertidal.

Cyatholaimidae

Pomponema mirabile Cobb; Sheepshead Shoal intertidal and below to depths of 15 cm. in sand; Fort Macon beach inside.

Gammanema ferox Cobb; Sheepshead Shoal, intertidal.

Synonchiella truncata Cobb; Bird, Sheepshead, and Guthrie Shoals at various levels; Lighthouse Bay, Cape Lookout.

Troglolaimus sp.; Sheepshead Shoal, bottom of tide pool.

Paracanthouchus sp.; several intertidal samples, Sheepshead Shoal; Guthrie Shoal; Lighthouse Bay, Cape Lookout.

Dispirella n. sp.; two species that were collected on Sheepshead Shoal, and once on Fort Macon Beach inside.

Dispira sp.; Sheepshead Shoal, intertidal. A new Dispira-like genus was also present in collections from the same habitat.

Axonchium-like new genus; Sheepshead Shoal, intertidal and at low tide mark.

Choanolaimus sp.; Sheepshead Shoal; intertidal.

Choanolaimus-like new genus; Sheepshead Shoal; low tide mark.

Tripyloididae

Bathylaimus sp.; several times on Sheepshead Shoal and Fort Macon beaches.

Tripyloides sp.; Sheepshead Shoal, intertidal.

Microlaimidae

Bolbolaimus cobbi Chitwood; several times on Sheepshead Shoal and Fort Macon beaches; intertidal and low tide mark.

Microlaimus sp.; Sheepshead Shoal, intertidal.

Chromadaridae

Neochromadara n. sp.; common in many collections from Sheepshead Shoal; also from Guthrie Shoal and Lighthouse Bay, Cape Lookout.

Odontonema-like new genus; several collections from Sheepshead Shoal and one from Fort Macon beach inside.

Desmodaridae

Dasynemella n. sp.; Sheepshead Shoal, 0.5 m. below low tide mark.

Monoposthia hexalata Chitwood; Sheepshead Shoal, low tide mark, 7 cm. deep in sand.

Dasynemoides n. sp.; Sheepshead Shoal, low tide mark, 7 cm. deep in sand.

Sporena-like new genus; Sheepshead Shoal, low tide mark, 7 cm. deep in sand.

Heterodesmodara-like new genus; Sheepshead Shoal, low tide mark to 0.7 m. below surface, on bottom of tide pool, and 7 cm. deep in sand.

Metachromadora cancellatus (Cobb); common on Sheepshead Shoal at various levels; Guthrie Shoal.

M. onyxoides Chitwood; several collections on beaches around Fort Macon at various levels and once on Sheepshead Shoal.

M. campycoma (Cobb); Fort Macon Beach outside, above high tide to low tide mark.

Enoplidae

Rhabdodemania minima Chitwood; intertidal, Lighthouse Bay, Cape Lookout.

Enoplolaimus sp. One species that belonged to this genus was found on Guthrie and Sheepshead Shoals between tides and at low tide mark; and on the beaches around Fort Macon from high tide to low tide mark. Another species occurred between tides in Lighthouse Bay, Cape Lookout; on Sheepshead Shoal between tides and at the bottom of a tide pool.

Enoploides labiatus (Bütchli); intertidal and 15 cm. deep in sand, Sheepshead Shoal.

Trefusia n. sp.; flats, Bird Shoal.

Oncholaimidae

Oncholaimoides striatum Chitwood; Sheepshead Shoal, between tides down to 0.5 m. deep and to depths of 15 cm. in sand; Guthrie Shoal, below low tide mark: intertidal, Lighthouse Bay, Cape Lookout.

O. rugosum Chitwood; Bird Shoal and Fort Macon inside, 0.5 m. below surface.

Oncholaimium appendiculatum? Cobb; Shipstake Shoal and Fort Macon outside, at and just below low tide mark.

Oncholaimellus n. sp.; common on Sheepshead Shoal at various levels and to depths of 15 cm. in sand; Lighthouse Bay, Cape Lookout, intertidal.

Viscosia brachylaimoides Chitwood; Sheepshead Shoal, intertidal at depth of 15 cm. in sand.

Viscosia n. sp.; Sheepshead Shoal and Fort Macon outside, intertidal.

Bolbella tenuidens Cobb; Bird and Sheepshead Shoals, intertidal, surface to depth of 15 cm. in sand.

Trilepta n. sp.; Sheepshead and Guthrie Shoals; intertidal and below, to depth of 15 cm. in sand.

Paraewrystomina typicum Micoletzky; Sheepshead Shoal and once from Fort Macon outside; mostly at and below low tide mark.

Iranidae

Trissonchulus n. sp.; Fort Macon outside; high tide mark and intertidal at depths of 15 cm. in sand.

Iranella prismatalaima Cobb; Sheepshead Shoal, intertidal at depth of 15 cm. in sand.

Annelida
Polychaeta

Many polychaetes were collected that have not been identified. Our collections are in the hands of Martha Clark, who will identify them in time, along with other collections from Beaufort that she is working up. The following list includes only a few of the species that occur on sand beaches. The fauna on the beaches along the open sea was quite different from that on shoals and protected beaches along sounds. C. G. Bookhout helped in the identification of some of our specimens.

Nereidae

Nereis limbata Ehlers is often associated with shell fragments on bottoms, but at Beaufort it occurred on protected beaches in sand. It was quite characteristic on Bird and Sheepshead Shoals, but was not encountered along the open sea.

Nephthydidae

Nephthys bucera Ehlers was collected by digging on flats on shoals and in sieves near the open sea. *N.*

incisa Malmgren was found once at a depth of 3 m. off Sheepshead Shoal.

Eunicidae

Diopatra cuprea (Bosc) was absent from wave-beaten shores along the open sea, but was often abundant on muddy flats and spread over sandy areas. At times its tubes were brought up in dredge hauls at 10-20 meters.

Lumbrinereis tenuis Verrill was common on Bird and Sheepshead Shoals. Along the open ocean it was found only in tide pools and at depths of 2-3 meters.

Arabella opalina Verrill was at times sifted from the sands on shoals in sounds.

Stauronereis pallidus Verrill was common in certain places on the flat beaches along the open sea outside Fort Macon (Stations IV, V) and was at times collected in similar situations on the beaches inside Fort Macon (I) and on Bird Shoal (VI).

Glycera americana Leidy was common on the flats of Bird and Sheepshead Shoals and in similar habitats inside Shackleford Bank and on Guthrie Shoal. *G. dibranchiata* Ehlers was collected once on the beach inside Fort Macon (Station I).

Sedentaria
Ariciidae

Aricia ornata Verrill occurred at times on flat beaches on Sheepshead and Guthrie Shoals, and the beach inside Fort Macon (Station I).

Scoloplos fragilis (Verrill) was found on the flats on Sheepshead Shoal; *S. robustus* (Verrill) was also taken there once.

Chaetopteridae

Chaetopterus pergamentaceus Cuvier in shallow waters was characteristic of black sands such as occurred on the flats of Bird and Sheepshead Shoals.

Terebellidae

Pista sp. was taken once at Station I.

Amphictenidae

Cistenides gouldi (Verrill) was found occasionally on the shoals in the sounds at Beaufort.

Opheliidae

Ophelina agilis Andrews occurred at times below low tide mark on Sheepshead Shoal.

Maldanidae

Petaloproctus socialis Andrews was often found at or below low tide mark along Bird and Sheepshead Shoals and was caught in dredge hauls at depths of 3-4 m. in the open sea off Fort Macon beach.

Clymenella torquata Leidy was abundant on the flats of Bird and Sheepshead Shoals, and occurred more or less on all flat, sandy beaches in the Beaufort region.

Arenicolidae

Arenicola marina (L.) was common on the flats on shoals, such as Bird and Sheepshead. Specimens were dug and egg strings that contained developing eggs were collected on Bird Shoal on December 7, 1941.

Serpulidae

Hyroides hexagonus Bosc attached to various objects was dredged in the open sea off the Fort Macon beaches at times.

Sabellariidae

Sabellaria vulgaris Verrill was sometimes found at low tide mark in sand tubes on Bird Shoal and at Station I.

Gephyrea
Priapulidea

Thalassema melitta Conn. This echiurid was often found in the empty tests of sand dollars (Mellita), and at times among Petaloproctus tubes and in old shells.

Sipunculidea

Sipunculus nudus L. was found in burrows in the sandy beaches along Bird and Sheepshead Shoals, and less commonly at Station I and on the margins of Shark Shoal and Shakleford Bank.

Arthropoda
Crustacea
Ostracoda

W. L. Tressler (1940) has kindly identified the ostracods we collected on sand beaches during the summer of 1939. He found eight species, and thus extends the range of several southward.

Cytheridae

Cytheridea papillosa Bosquet occurred on Sheepshead Shoal. *C. ruba* G. W. Muller was more common and widely distributed on Sheepshead and other shoals, and on the beach at Station I.

Cythere viridis O. F. Muller was present on shoals in Beaufort sounds. *C. albomaculata* Baird was collected on Sheepshead Shoal and on the beach along the open sea (Station V).

Xenothythere cuneiformis Brady occurred in tide pools and on Sheepshead Shoal.

Cytherura striata G. O. Sars was found on several shoals in sounds and at Station I.

Xestoleberis aurantia (?) (Baird) occurred as immature specimens on shoals.

Cytherois pusilla G. O. Sars was collected on Sheepshead Shoal, where it was apparently common.

Copepoda

All copepods from Beaufort sand beaches have been sent to Donald J. Zinn, who expects to identify them when he finds time. General results of collections in salve boxes are shown in Table 4.

Malacostraca
Mysidacida

Michtheimysis stenolepis Smith was often taken in seine hauls and at times in salve box samples on beaches along the open sea and on shoals in sounds.

Cumacea

Diastylis quadrispinosus G. O. Sars was taken once in a sand sample from a depth of 3 m. in the channel near Shackleford Bank, June 30, 1941.

Cyclaspis varians Calman was collected once (a young female) in a sieve on Shipstake Shoal, June 14, 1939.

Amphipoda

Many of the amphipods were identified by Clarence R. Shoemaker, whose prompt and efficient help is greatly appreciated.

Lysianassidae

Lysianopsis alba Holmes; a specimen was caught in a dredge at a depth of 2 m. in the open sea off Shackleford Bank.

Ampeliscidae

Ampelisca macrocephala Lillj. was collected on Bird Shoal, July 23, 1941.

Haustoriidae

Haustorius sp. was abundant on shoals and often common on exposed ocean beaches (Tables 4, 5). Mr. Shoemaker believes that species on the Atlantic coast need revision, and is not willing to give those we collected a specific name.

Phoxocephalidae

Pontharpina floridana Shoemaker was rather common below low tide mark in sounds. It was often brought up in sand secured with a diving hood at depths of 3-4 m.

Leucothoidae

Leucothoe spinicarpa Abildgaard was taken in a dredge haul off Shackleford Bank at a depth 2-3 m.

Atylidae

Nototropsis minikoi (A. O. Walker) was collected on beaches along the open sea in the summers of 1939 and 1941, near or below low tide mark.

Gammaridae

Carinogammarus mucronatus (Say); Station V, June 13, 1941; in seine.

Mellita fresnelii (Audouin) was taken in dredge hauls in sounds and channels. It appeared often to be associated with the ascidian, *Styela partita*.

Talitridae

Orchestia grillus (Bosc) was at times at and above high tide mark on the beaches both inside and outside Fort Macon, but was more common along grassy margins on Shark Shoal and Shackleford Bank.

Talorchestia megalophthalmia (Bate) was collected at and above high tide mark on beaches near Fort Macon.

Aoridae

Lembos smithi Holmes; dredge, off Shakleford Bank, 2-3 m., August 7, 1941.

Amphithoidae

Amphithoë longimana (Smith) was seined on the beach outside Fort Macon.

Corophiidae

Unciola irrorata Say; dredge at 2-3 m. along tip of Shackleford Bank, August 7, 1941.

Caprellidae

Caprella acutifrons Latreille; many taken with algae in seine hauls on Fort Macon beach outside, June 12. 1941.

Isopoda
Anthuridae

Cyathura carinata (Kroyer) was taken in sieves on flat shoals in sounds.

Cirolanidae

Cirolana concharum (Stimpson) was taken once in a sieve inside Shackleford Bank and once while diving at 7 m. off Fort Macon.

Cymothoidae

Irona nana Schioedte & Meinert; seine along Bird Shoal, June 2, 1941; parasitic on fishes.

Idotheidae

Chiridotea caeca (Say); quite common on sand beaches, and a characteristic type in the intertidal zone at all stations, and at depths of 3-5 m. off Fort Macon.

Bopyridae

Probopyrus latreuticola (Gissler) occurred in the gill chambers of two shrimps, *Latreutes ensiferus* (Milne-Edwards) caught in the surf at Station V (Fig. 1) July 19, 1941.

Ligydidae

Ligyda exotica (Roux). This species is usually found running about on walls and piles above the sea, but on June 12, 1941, a single individual was found under a board on the beach outside Fort Macon (Station IV).

Stomatopoda

Chloridella empusa (Say). Several erichthus larvae, probably of this stomatopod, were caught in sieves and seines outside Fort Macon (Station V), July 14, 15, 1939. Adults were often taken in trawls off Fort Macon in the open sea and one was thus collected near Bird Shoal.

Lysiosquilla excavatrix (Roux) (Figs. 10, 13) was quite common on the flat beaches on Bird Shoal and outside Fort Macon. Once one was found in the same burrow with a Calianassa.

Decapoda
Peneidae

Peneus brasiliensis Latreille. This large shrimp was often taken in trawls over sea bottoms off Fort Macon and at times was present in seine hauls on shoals in sounds or on shallow beaches. Fishing boats regularly leave Beaufort to trawl for shrimps in the sea near by.

Parapenaeus politus Smith; two specimens in dredge off Fort Macon, at depth of 3 m., July 16, 1941.

Ogyridae

Ogyris alphaerostris Kingsley (Figs. 10, 12). This shrimp which was believed to be rare we found to be quite common at Station V (Fig. 1) in a rather firm bottom of dark gray sand at a depth of about 1 m. It was also found in a similar habitat along the shore of Bird Shoal; and once on the highest part of that shoal.

Hippolytidae

Latreutes ensiferus (H. Milne-Edwards) was found on the beach outside Fort Macon, especially when Sargassum and other algae were blown inshore.

Cragonidae

Crago septemspinosus (Say); along Bird Shoal, in seine and rake net.

Porcellanidae

Polyonyx macrocheles (Gibbes) usually was found only in Chaetopterus tubes, but once was seined on the beach outside Fort Macon.

Euceramus praelongus Stimpson was not common, but was collected at times at low tide mark on the landward side of Bird Shoal, especially near the channel between it and Sheepshead Shoal; also dredge along Shackleford Bank.

Callianassidae

Callianassa major (Say) (Fig. 10) was very common on flat sand beaches on Bird and Sheepshead Shoals and in similar situations outside Fort Macon. It lives in burrows a meter or more deep. Females were carrying eggs throughout June and at least during the early part of July, 1941.

Paguridae

Clibanarius vittatus (Bosc); this large hermit crab was not uncommon along the shores of Shark and Bird Shoals and along protected beaches on Shackleford Bank.

Pagurus pollicaris Say; more characteristic in deep water, but often found on beaches, especially along the open sea.

Pagurus longicarpus Say; often abundant on sand beaches, especially along Bird and Sheepshead Shoals; also common in channels in Beaufort Harbor.

Albuneidae

Albunea gibbesii Stimpson; Bird and Sheepshead Shoals, near low tide mark.

Lepidopa websteri Benedict (Figs. 10, 11); most common at or just below low tide mark along the open sea (Stations IV, V), but also found on the beach inside Fort Macon and once on Bird Shoal. In 1941 small individuals were taken on July 21; ovigerous females July 10, 12, 22.

Hippidae

Emerita talpoida (Say) (Figs. 10, 16) was very common on sandy, wave-swept beaches. It has been considered in detail by Wharton earlier in this paper.

Calappidae

Hepatus epheliticus (L.). From trawl hauls in the open ocean the Dolly Varden crab appeared to be more abundant in deep (15 m.) than in shallow (3.5 m.) water.

Leucosiidae

Persephona punctata (L.). The purse crab was found on exposed sand beaches after onshore winds, but was more often caught in trawls in deep water (7-15 m.). An ovigerous female was dug up between tides on the beach outside Fort Macon June 26, and another caught at a depth of 15 m. on July 10, 1941.

Portunidae

Ovalipes ocellatus ocellatus (Herbst) (Fig. 10). The lady crab was quite common, especially along the open sea; it also was taken commonly in trawl hauls (3-15 m. deep).

Portunus gibbesii (Stimpson); taken once on Sheepshead Shoal.

P. sayi (Gibbes), at times washed in with Sargassum by onshore winds.

P. spinimanus Latreille; taken once in a dredge near Sheepshead Shoal.

P. spinicarpus Stimpson; taken in seine and rake-net hauls on beaches outside Fort Macon.

Callinectes sapidus Rathbun; abundant on beaches and in deep water near Beaufort, and even ranging into freshwater.

C. ornatus Ordway; not common, but caught at times along Bird and Sheepshead Shoals.

Arenaeus cribrarius (Lamarck); common at low tide mark and often captured in rake-net catches, especially along the open sea.

Xanthidae

Neopanope texana sayi (Smith); in dredge hauls in channels or outside the banks, often among ascidians, oysters, or other groups of animals.

Pinnotheridae

Dissodactylus mellitae (Rathbun); often found on sand dollars (Mellita).

Pinniza cristata Rathbun; rather common on sand flats, in various worm tubes, and in Callianassa burrows.

Ocypodidae

Ocypode albicans Bosc (Fig. 10). The ghost crab is common above high tide mark along the open sea. Young individuals often dig burrows in the intertidal zone. The crabs are abundant on beaches at night, but usually remain in their burrows during the day. Some individuals dig burrows in sand dunes at considerable distances from the sea.

Uca pugilator (Bosc). The sand fiddler is not characteristic of sand beaches, but sometimes wanders onto them from its usual habitats where bottoms are suitable for its burrows by the presence of clay or the roots of shore plants.

Inachidae

Podochela riisei Stimpson; one specimen caught in trawl outside Fort Macon at a depth of 14 m.

Metoporhaphis calcaratus (Say); sometimes cast on beach with algae by onshore winds.

Libinia dubia H. Milne-Edwards; often taken in dredge or trawl offshore and at times in seine hauls on the beaches near Fort Macon.

Parthenopidae

Heterocrypta granulata (Gibbes). A hexagon crab was taken once in a sandy bay on Shark Shoal, and several specimens were dredged near Shackleford Bank.

Insecta
Coleoptera
Cincindelidae

Cincindela dorsalis media Lec. was a common hunter on all sandy beaches. Three tiger beetle larvae that Dr. Manson Valentine believes may perhaps belong to this species were in the sand beach inside Fort Macon (Station II, Fig. 1) June 5, 1941. These were covered by sea water at each high tide. Dr. Valentine also identified another tiger beetle (*C. hirticollis* Say) that hunts on flats that do not border the ocean near Fort Macon.

Staphylinidae

Staphylinid and other beetles were often found along the drift line. Doubtless these were scavengers, and some perhaps predators.

Diptera
Asilidae

Laphystia litoralis Curran. This little robber fly was abundant along the sand beaches. Mr. Charles T. Greene, who identified specimens, says that it is common on beaches. It was present through the summer of 1941, and was observed in numbers September 10 and December 7.

Dolichopodidae

Hypocharassus gladiator Lec. or *H. pruniosus* Wh. Larvae that Mr. Greene believes belong to one of these species were found in the flats on Bird Shoal June 1 (3) and 14 (1), 1941. They were covered with sea water every time the tide rose. Other fly larvae were found a few times in salt water beaches, but attempts to rear them were unsuccessful.

Sympycnus sp. was common on the algae cast up on the beach outside Fort Macon, September 10, 1941.

Xiphosura

Limulus polyphemus L. Pairs of king crabs were often seen during June and July in the sand on Bird and Sheepshead Shoals, but were not observed on the beaches about Fort Macon. Small individuals were common on the flats west of the shoals.

Arachnida
Araneida

Lycosa cinerea (L.) (?) was often seen along sandy beaches that were bordered by dunes.

Acarina

An unidentified mite was found in a salve box sample at Station II (Fig. 1) July 10, 1939; taken 0.5 m. under water.

Mollusca
Pelecypoda
Solemyidae

Solemya velum Say was common in "black sand" on shoals; not in mud and not in sand on wave-swept beaches.

Arcidae

Arca campechiensis Gmelin was found on Guthrie Shoal along shore.

Pinnidae

Atrina rigida Dillwyn was not uncommon on sandy to muddy flats that were covered at high tide.

Ostreidae

Ostrea virginica Gmelin was not an inhabitant of sand beaches but was at times brought up in dredge hauls over them. It of course requires solid objects for attachment.

Pectinidae

Pecten gibbus L. was at times present on the sand flats of Bird Shoal. It is usually associated with eel grass or other vegetation.

Lucinidae

Divaricella quadrisulcata D'Orbigny; collected once on Bird and Sheepshead Shoals, and on the beach inside Fort Macon.

Cardiidae

Cardium robustum Solander (Fig. 8) was most often taken at low tide mark along the channel at the north end of Shackleford Bank, but was also sometimes found on Bird, Sheepshead, and Guthrie Shoals.

Veneridae

Dosinia discus Reeve (Fig. 8); along margins of Bird and Guthrie Shoals.

Macrocallista nimbosa (Solander) (Fig. 8); found on the flats of Bird and Sheepshead Shoals.

Chione cancellata (L.); Bird, Sheepshead, and Guthrie Shoals.

Venus mercenaria L. (Fig. 8). The quahog was quite common on mud and sand flats on Bird, Sheepshead, and Guthrie Shoals and also occurred on the beach inside Fort Macon.

Gemma gemma L.; taken twice on Shipstake Shoal; June 20, July 27, 1939.

Petricolidae

Petricola pholadiformis Lamarck; Sheepshead Shoal; August 3, 1939.

Tellinidae

Tellina tenera Say; Bird, Shipstake, and Guthrie Shoals, Fort Macon beaches inside and outside, Lighthouse Bay at Cape Lookout.

Donacidae

Donax variabilis Say (Fig. 8) was abundant on the wave-swept beaches about Beaufort (Table 5); more abundant on the beach inside Fort Macon than outside or on Bird and Sheepshead Shoals.

Sanguinolariidae

Tagelus gibbus (Spengler) (Fig. 8) was characteristic of firm mud beaches but occurred along the borders of sandy areas on Bird and Sheepshead Shoals.

Solenidae

Ensis directus Conrad is not common about Beaufort and does not grow as large as in more northerly latitudes, but was found on Bird, Shark, and Guthrie Shoals.

Mactridae

Spissula solidissima Dillwyn was rather common on Bird and Sheepshead Shoals, along Shackleford Bank, and outside Fort Macon.

Gastropoda
Naticidae

Polinices duplicata (Say) (Fig. 4); rather common on Bird, Sheepshead, and Guthrie Shoals, and found outside Fort Macon from the beach down to a depth of 17 m.

Sinum perspectivum Say (Fig. 4); often collected along Bird and Sheepshead Shoals, also found on the beach outside Fort Macon and inside Shackleford Bank.

Crepidulidae

Crepidula fornicata (L.); common on the exoskeletons of Limulus, and often brought up in dredge hauls attached to various hard objects.

Crepidula plana Say; often seen in the shells occupied by large hermit crabs.

Pyrenidae

Anachis avara Say; at times collected below low tide mark outside Fort Macon, usually in dredge hauls.

Nassaridae

Nassarius obsoleta Say; very abundant on muddy flats and protected shores and occasionally spreads over sand beaches.

N. trivitata (Say); characteristic and fairly common on sandy shoals (Sheepshead, Shipstake, Guthrie).

N. vibex Say; not as common as *N. trivitata* on sand beaches along shoals and occurs at a somewhat lower level, at and below low tide mark.

Neptuneidae

Busycon carica carica Gmelin. This large snail was often found on Bird, Sheepshead, Guthrie, and Shipstake Shoals, and also was not uncommon on the flat sand beaches outside Fort Macon.

Olividae

Oliva sayana sayana Ravenel (Figs. 4, 5, 6); along borders of sandy shoals and beaches along the open ocean where there were currents and waves.

Olivella mutica Say, *O. floralia* Duclos. These little snails were at times abundant at low tide mark on flat sandy beaches along Bird and Shipstake Shoals and Shackleford Bank. They were also dredged at 2-7 m. off Fort Macon beaches.

Terebridae

Terebra dislocata dislocata Say (Figs. 4, 7) was quite common on shoals and flat, protected beaches; most numerous just below and at low tide mark.

Aplysiidae

Tethys sp. was at times taken on the beach outside Fort Macon and on Sheepshead Shoal after storms. Mr. L. G. Williams says that it commonly associated with and feeds on an alga (Codium).

Scyllaeidae

Scyllaea pelagica marginata Bergh; blown on beach outside Fort Macon with Sargassum, July 18, 19, 1941.

Cephalopoda
Loliginidae

Loligo pealeii pealeii Le Sueur; commonly caught in trawls in channels within Beaufort Harbor and in the open ocean at various depths, to 15 m. or more. This squid evidently hunts over sand bottoms.

Echinodermata
Asteroidea
Astropectinidae

Astropecten articulatus (Say); taken in dredges and trawls at depths of 3-14 m. in the ocean outside Fort Macon.

Luidia clathrata (Say); in shallow water on the beaches around Fort Macon; one caught in a rake net haul and another picked out of a tide pool.

Asteriidae

Asterias forbesii Desor. Specimens were occasionally found on the beaches inside and outside Fort Macon, and in trawl hauls offshore.

Ophiuroidea
Ophiodermatidae

Ophioderma brevispina Lutken; beach inside Fort Macon; Guthrie Shoal.

Amphiuridae

Ophiopholis aculeata (L.); collected several times in the sands of Bird Shoal and once on Shackleford Beach.

Ophiogramus wundermanni (Lyman) was reported at Beaufort long ago by Grave (1902). We collected it twice on Bird Shoal in or near "eel" grass *(Ruppia maritima)*.

Amphiopholis gracillima (Stimpson) was collected once on the beach inside Fort Macon at low tide mark in a sieve.

Echinoidea
Arbaciidae

Arbacia punctulata (Lamarck) was often taken in dredge and trawl hauls in sounds and sometimes in the open sea, but was not particularly characteristic of sand beaches, and was rarely found on them.

Scutellidae

Mellita quinquiesperforata (Leske) was very abundant in sounds along the shores of shoals and was often taken in numbers in dredge hauls in deep water. It was very characteristic on sand beaches, at and below low water mark (Tables 7, 8).

Hemiastridae

Moira atropos (Lamarck); common on the mud-sand margin of a channel through Bird Shoal, and sometimes on clean sandy beaches there; also found on Guthrie Shoal. The heart-urchin is usually found 10-20 cm. below the surface of the sand.

Holothuroidea
Cucumariidae

Cucumaria pulcherrima (Ayers); not common about Beaufort, and usually attached to solid objects, but collected once on Bird Shoal.

Thyone briareus (Le Sueur); often on the beach outside Fort Macon after strong onshore winds; also found three times on Guthrie Shoal and once on Shackleford Bank. This sea cucumber probably usually lives a little below low tide mark, where it secures food but escapes violent wave action.

Synaptidae

Leptosynapta inhaerens (O. F. Müller); Bird, Sheepshead, Guthrie, and Shark Shoals; Lighthouse Bay, Cape Lookout; Shackleford Bank beach. This is a burrowing sea cucumber that is quite characteristic on sand beaches.

Enteropneusta

Balanoglossus auranticus (Girard). This big enteropneustan was abundant on muddy and to some extent on clear sand flats; its fecal piles were quite diagnostic and even its burrows had a characteristic fetid odor. It was scattered over the flats of Bird and Sheepshead Shoals and occurred along the beach inside Fort Macon.

Chordata
Tunicata
Synoicidae

Amaroecium constellatum Verrill; at times cast on the beach outside Fort Macon during storms.

Ascidiidae

Phallusia hygomiana Trausdet; collected in rake net along margin of Sheepshead Shoal and in dredge twice off Fort Macon beach outside at a depth of 3 m.

Botryllidae

Botryllus sp.; Fort Macon beach outside, on beach after onshore wind, caught in seine and dredge (3 m.).

Styela plicata (Le Sueur); attached to piles, oysters, shells, and other solid objects; often taken in dredge hauls over sandy bottoms.

Leptocardia
Branchiostomidae

Branchiostoma virginiae Hubbs. A few specimens have been reported from collectors in the past for the Beaufort region, all taken in shallow water. During the summer of 1941 we collected eight individuals, all with diving hood and dredge from sand taken at depths of 3-4 m. near Bird and Sheepshead Shoals and Shackleford Bank.

Elasmobranchii
Carchariidae

Carcharias littoralis (Mitchell). Sand sharks were rather common about Beaufort Harbor. Once when Wharton was wearing a diving hood in 7 m. of water off Fort Macon a 1.5 m. shark came along and persistently smelled his stomach.

Dasytidae

Dasyatis americana Hildebrand & Schroeder. The southern sting ray was quite common on sandy and muddy bottoms, and was often caught on hooks and at times in trawls.

Peroplatea micrura (Schneider) often caught in trawls; along Sheepshead Shoal and over sand bottoms in the open sea; food includes fish, shrimp, clam, etc.

Teleostomi
Engraulidae

Anchoviella mitchilli (Cuvier & Valenciennes). Anchovies were often caught in seine hauls (Table 6).

Synodontidae

Synodus faetens (L.). Lizard fishes never occurred in great numbers but were often present along more or less protected beaches (Table 6).

Poeciliidae

Fundulus majalis (Walbaum) was often so abundant on sand beaches that it made veritable clouds. Schools wiggled over flats in water that was shallower than the thickness of their bodies as flats were gradually covered by rising tides (Table 6). *F. heteroclitus* (L.) was not common on sand beaches.

Hemirhamphidae

Hyporhampus unifasciatus (Ranzani). Small half-beaks were collected twice in seine hauls; Shark Shoal, Bird Shoal.

Syngnathidae

Syngnathus fuscus Storer. Pipefishes were taken at times on the Fort Macon beaches (Table 6).

Atherinidae

Menidia menidia (L.). Silversides were the commonest fishes along sand beaches (Table 6).

Mugilidae

Mugil cephalus L. The striped mullet is one of the commercial fishes seined by fishermen along sandy beaches about Beaufort.

Sphyraenidae

Sphyraema borealis De Kay; 1 small specimen seined on beach inside Fort Macon.

Scombridae

Scomber scombrus L.; in one seine haul 235 small mackerel were caught on the beach inside Fort Macon, June 5, 1941.

Gemphlidae

Trichiurus lepturus L. Cutlass fishes were often caught in trawling outside Fort Macon (15-20 m.).

Carangidae

Caranx hippos L. Jacks were often seined on sand beaches (Table 6).

Alectis ciliaris (Bloch); two individuals in 1941; south end of Shark Shoal, June 19; trawl at 7 m. off Fort Macon, July 10.

Trichonotus carolinus (L.); small pompano were seined several times on the Fort Macon and Shackleford beaches during June and July.

Pomatomidae

Pomatomus saltatrix (L.); 2 small bluefish, beach outside Fort Macon, seine June 28, 1941.

Stromateidae

Poronotus tricanthus (Peck); butterfish was often taken in trawls off Fort Macon.

Serranidae

Centropristus striatus (L.); in trawls off Fort Macon.

Sparidae

Lagodon rhomboides (L.); pinfish (Table 6) was seined alongshore and commonly caught in trawls.

Sciaenidae

Cynoscion regalis (Bloch & Schneider); weakfish, or sea trout, were taken in trawls outside Fort Macon at times.

Leiostomus xanthurus Lacepede; spots were commonly taken in trawls, and at times seined on beaches (Table 6).

Micropogon undulatus (L.); croakers were often caught in trawls and seines (Table 6).

Menticirrhus americanus (L.); kingfishes were often seined in small numbers on sand beaches (Table 6).

Labridae

Lachnolaismus maximus (Walbaum); trawl, off Fort Macon, 15 m.

Balistidae

Balistes carolinensis Gmelin; small triggerfishes were often taken in seines (Table 6) and at times in trawls in deep water outside Fort Macon.

Triglidae

Prionotus carolinus (L.). Sea robins were rather common on sandy beaches and many could be seen on the bottom in moderate depths (3-7 m.) on sandy bottoms, when observations were made by using a diving hood. *P. scitulus* Jordan was also present.

Uranoscopidae

Astroscopus y-graecum (Cuvier & Valenciennes). A stargazer was brought in during the summer of 1941 and exhibited in the aquarium of the Fish and Wild Life Service. As this fish remains buried in sand and is difficult to catch, its abundance is not known. Smith (1907) reported it from Bird Shoal.

Blennidae

Hyposoblennius hentz (Le Sueur). The Carolina blenny was found once on Sheepshead Shoal among a cluster of Clymenella tubes.

Pleuronectidae

Paralichthys dentatus (L.). This flatfish was rather common along sandy beaches (Table 6) and was often taken in trawls in deeper water.

Paralichthys albigutulus Jordan & Gilbert; at times caught in seines (Table 6) and trawls.

Ancylopsetta quadrocellata Gill; this fluke was not as common on sand beaches as the last two.

Lophopsetta maculata (Mitchill); July 17, 1939, four sundials were caught in trawl hauls off Fort Macon at a depth of 7 m.

Soleidae

Symphurus plagiusia (L.); one tonguefish was caught in a rake net at a depth of 1 m. at the south end of Shark Shoal, June 19, 1941; two others were caught in a trawl (14 m.) off Fort Macon, July 10, 1941.

Antennariidae

Histrio histrio (L.); a sargassum fish was caught in the surf on the beach outside Fort Macon, July 19, 1941.

Aves
Pelecanidae

Pelicanus occidentalis occidentalis L. Brown pelicans were sometimes present in the sounds and on the flats about Beaufort, never more than 3 or 4 at a time.

Ardeidae

Ardea herodias L. The great blue heron was to be seen at times throughout the summer. It fished along the edges of marshes and sand beaches.

Florida caerulea caerulea (L.). Little blue herons were fishing throughout the summer. The snowy white young were commoner than the blue elders. Nests were found in the marshes.

Hydranassa tricolor ruficollis (Gosse). Louisiana herons at times were seen fishing along marshes and sand beaches.

Butroides virescens virescens (L.). Green herons were seen at times in marshes.

Cathartidae

Coragyps atratus atratus (Bechstein). Black vultures at times fed on stranded carcasses along the shores of marshes and sand beaches.

Buteoninae

Haliaeetus leucocephalus (L.). Bald eagles were at times seen robbing fish hawks and resting on sand beaches.

Pandioninae

Pandion haliaetus carolinensis Gmelin. Ospreys fished in the ocean along sand beaches, where they were not as common as on the coasts of Florida.

Carardriidae

Charadrius wilsonia wilsonia Ord. Wilson's plover picked Emerita and Donax out of sand beaches when tides left them exposed.

Scolopacidae

Catoptrophorus semipalmatus (Gmelin). Willets often hunted on sand beaches.

Ereunetes pusillus (L.). Semipalmated sandpipers commonly probed sand beaches for food.

Larinae

Larus argentatus Pontoppidan. Herring gulls are very abundant in winter. They sit on piers and sand beaches in great numbers. Their feces contribute to the organic food resources in sand beaches.

Larus atricilla L. Laughing gulls are common in summer about beaches and their excreta add to the organic materials in sand.

Sternidae

Sterna hirundo hirundo L. Common terns are a regular part of the summer population of the Beaufort region.

Sterna albifrons antillarum (Lesson). Least terns are abundant summer residents. They nest on Shark Shoal and other bare sandy areas.

Thalasseus maximus maximus (Boddaert). Royal terns are common summer residents.

Hydroprogne tschegrava (Lepechin). Caspian terns are common summer residents.

Rynchopidae

Rynchops nigra nigra L. Skimmers commonly fish in flocks along sand beaches. They nest on Shark Shoal.

Corvidae

Corvus ossifragus Wilson. Fish crows were not common at Beaufort, but were at times seen along beaches.

Icteridae

Cassidix mexicanus major (Vieillot). Boat-tailed grackles roosted in the trees on Piver's Island and commonly hunted food along beaches.

Mammalia
Delphinidae

Tursiops tursio (Fabricius). Dolphins are seen daily in sounds and along beaches about Beaufort.

Gobiocephala melas (Traill). Blackfish at times become stranded on the ocean beaches at Beaufort.

ECOLOGICAL FACTORS INFLUENCING REFORESTATION
IN NORTHERN WISCONSIN

JOSEPH H. STOECKELER
Lake States Forest Experiment Station,*
United States Forest Service

and

GUSTAF A. LIMSTROM
Nicolet National Forest, United States Forest
Service, Rhinelander, Wisconsin

hcB

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ECOLOGICAL FACTORS INFLUENCING REFORESTATION IN NORTHERN WISCONSIN

INTRODUCTION

In recent years considerable attention has been devoted in the United States to a large-scale effort in reforestation of land devastated by fire and destructive logging. Among the major forest regions of the country, few have been devastated as extensively as the Lake States,[1] and as a consequence these states have the largest reforestation program of any forest area in the United States.

In 1940, for example, out of a total of 146,982 acres of trees planted in the national forests within the continental United States, 67,491 acres were planted in the three Lake States. To produce the stock needed for this area required the output of 12 forest nurseries with an annual production of about 73 million plantable trees.

To attain maximum success of the reforestation efforts at reasonable cost requires a thorough grasp of the ecological factors involved, and such factors can most quickly be segregated and weighted by experimental planting done over a period of years under a wide range of soil, cover, and climatic conditions.

The present paper on ecological factors and the development of young forest plantings is based on the results of experiments conducted from 1937 to 1940, inclusive. It does not attempt to cover all sites but is limited largely to the light sandy soils which formerly supported extensive forests of red and white pines.

REVIEW OF LITERATURE

The most extensive compilation of data on forest planting in the Lake States was made by Kittredge (1929). He emphasizes the importance of climatic conditions and states that in years of marked deficiency of rainfall, first-year losses may exceed 50 percent.

Rudolf (1937) found drought losses accounted for 87 percent of all mortality during the severe drought year of 1933 in the Huron National Forest in lower Michigan. In 1936 a severe drought was accompanied by unusual heat, and soil-surface temperatures reached a maximum of 175°F. and in one record showed temperatures over 130°F. for 8½ consecutive hours. In ten young jack pine plantings, heat caused 74 percent of the mortality and drought 26 percent.

Münch (1915), Hartley (1918), Korstian and Fetherolf (1921), Toumey and Neethling (1923), Bates and Roeser (1924), and Baker (1929) have shown soil-surface temperature to be a factor contributing to mortality of young forest seedlings. The average temperature above which considerable mor-

tality occurs lies between 120° and 140°F. but the work of these writers shows that it may vary in the extreme range of 96°F. to 180°F. depending on length of exposure, species, and age of seedlings. Temperatures of 170° to 180°F. can be endured for only a short period.

Slope and exposure are important factors in probability of heat injury. Bates and Roeser (1924) state that in the Rocky Mountain region, surface temperatures on exposed southerly slopes may reach maxima of 150° to 160°F., while on north slopes they seldom exceed 110°F. Pool (1914) found a similar contrast in the Nebraska sandhills with surface temperatures of 91.5° and 145°F., respectively, on north and south slopes.

Moisture content of soil strongly influences surface temperature. Wollny (1880) states that moisture increases evaporation, which in turn has a pronounced cooling effect on surface temperature. This is of especial importance in shallow-water-table areas, as will be brought out in this paper presently.

Soil moisture content is one of the most important factors in success or failure of seeding and planting and is intimately correlated with normality and distribution of rainfall, water-holding capacity of soil, and intensity of plant competition. Toumey and Kienholz (1931) showed that decreased moisture content due to root competition not only slows up growth but may even result in death of small seedlings.

Larsen (1940) found much greater soil moisture in the top foot of soil on northwest and northeast slopes than on southwest slopes. Flat land was usually intermediate in soil moisture content. Soil moisture conditions were often so poor on southwest slopes that survivals were low enough to consider the plantings as failures. On the moister north-facing slopes or on flats the survivals were usually good.

Show (1930) states that in dry years on California forest planting sites, total soil moisture content of the top 6 inches of soil may drop below 5 percent from the middle of July to the end of September, while in wet years it remained above 7 percent throughout the season.

The method of ground preparation is an important factor in survival and growth, because adequate ground preparation reduces competition for moisture, light, and nutrients. In the Lake States, plantation survival is often 10 to 20 percent higher on droughty sites, where plants are set in plowed furrows rather than in spots prepared by scalping.[2] Shirley (1937) states that reduction of competition by adequate ground preparation is an absolute necessity for suc-

[1] By Lake States region as here used is meant Michigan, Wisconsin, and Minnesota.

[2] The term "scalping" refers to removal of sod and herbaceous vegetation on a spot from 1 to 2 feet square and to a depth of 1 to 2 inches.

cessful direct seeding, and condemns broadcast sowing on sites with heavy competition.

In subhumid prairie regions, summer fallow is often used to store up moisture for tree shelterbelts. Stoeckeler and Bates (1939) found that fallow land in midsummer had as much as 9 inches of water available in the top 8 feet of soil, wheatland had 2 to 3 inches, and pastureland as little as 0.3 inch of free water.

The presence of shallow water tables has a marked influence on distribution of natural vegetation as shown by Meinzer (1927) and may be of local significance in success or failure of reforestation by seeding, as shown by Stoeckeler and Sump (1940). Lyon and Fippin (1910) cite an experiment by Briggs who found the limit of capillary rise in a dry, fine sandy loam to be 15 inches in 14 days, while in the same soil in a somewhat moistened condition the rise was 66 inches, or 4.5 times that in the dry soil.

Comparative fertility and water relations of soil and nutrient requirements of individual species are in many instances of great importance in success or failure of reforestation. Kellogg (1936) shows the broad relationship between the great soil groups of the United States and existing natural vegetation and has shown correlation of forest types and soil types in an earlier study conducted in Wisconsin (1930). Korstian and Baker (1925) in discussing forest planting in the Intermountain region recommend that the occurrence and development of native species growing on or adjacent to a planting site should largely govern choice of species, and that native species should have preference over exotics. Wilde (1935) showed the relation of forest type to texture of soil and later (1938) showed that there existed a definite gradient of soil nutrients in stands of jack pine up through red pine and white pine to white spruce and hardwoods, such as sugar maple, basswood, and yellow birch.

From the viewpoint of initial success in reforestation, survival is usually enhanced by a thin overstory of more advanced forest growth or even brush. This is particularly true on sites where there is intense solar radiation, low rainfall during the growing season, or where sod tends to encroach vigorously on the site in the absence of an overstory. Wahlenberg (1930) found under a cover of Ceanothus brush that ponderosa pine had a first-year survival of 89 percent, while in the open it was only 53 percent. Maximum surface temperature was 51°F. higher in the open than under shade, and available soil moisture was 3.2 percent higher under the brush cover.

In the New England states where drought is not ordinarily a serious factor in mortality of young plantations, Kimball and Carter (1913) found a marked increase in survival of young white pine plantations in a dry season under cover of brush and small broadleaf saplings.

The general consensus of opinion based on experience and experimental evidence is that partial shade usually benefits early survival but may be dis-

tinctly detrimental to the more intolerant species a few years after planting. Byers (1926) cites a striking example of benefit by cutting of scrub oak in an experimental white pine plantation in Pennsylvania. Survival in 1926 of planting done in 1912 showed an estimated survival of only 20 percent in pine under a dense cover of scrub oak. In four other plots where various types of liberation cutting were made in 1919, survival ranged from 50 to 65 percent. Maximum growth was attained in the clear-cut plot. He concluded that in the long run not over 15 percent of 3-0 white pine planted on scrub oak sites would fight their way through the canopy of oak. There is a great range in light requirement of forest trees as pointed out by Toumey and Korstian (1937) and Baker (1934). Gast (1930) found terminal growth of white pine to be closely correlated with continuously recorded measurements of light, with poorest growth noted under comparatively low light intensity. Similar trends were found for red pine by Shirley (1932).

Some of the difference in success of reforestation depends on whether it is done by seeding or planting and is further affected by the age class and size of stock, top-root ratio, nutrient balance, and handling of trees from the nursery site to the field planting site. Larsen (1940), Rudolf and Gevorkiantz (1935), Bates and Pierce (1913), Tillotson (1915), Toumey and Korstian (1942), and numerous other investigators have pointed out the consistent superiority of transplant nursery stock over seedling trees in survival or growth in sites where soil moisture is a limiting factor or where competition by other plants is severe.

Biotic factors loom large in the probable chance of success or failure of reforestation efforts. Mice and chipmunks are responsible for much of the failure of direct seeding of conifers, as pointed out by Toumey and Korstian (1942). Kittredge (1929) cites cases where over half of a large number of white pine plantations in northern Minnesota had over 70 percent of the trees cut back by snowshoe hares and cottontail rabbits. Hayes and Wakeley (1929) observed that in some slash pine plantings in Louisiana over 80 percent of the trees were cut back by rabbits. The decreased vigor of trees and actual mortality are such that the potential value of the plantation may be severely reduced.

THE STUDY AREA: ITS CLIMATE, PHYSIOGRAPHY, COVER, AND SOIL

The area in which the present studies were conducted is located in Oconto County in northeastern Wisconsin, close to the village of Mountain, and is within the boundaries of the Nicolet National Forest.

The mean annual precipitation for a nearby U. S. Weather Bureau Station, 10 miles to the northeast, at High Falls, Wisconsin, for 1912 to 1938, inclusive, and the average number of days with 0.01 inch or more of precipitation are given in Table 1.

This section of Wisconsin has cold winters and

TABLE 1. Climatic data for High Falls, Wisconsin.[1]

	Length of record years	Jan.	Feb.	Mar.	Apr.	May	June
Mean precipitation, inches	[2]27	1.36	1.36	1.86	2.56	2.76	3.65
Average number of days with 0.01 or more inches of precipitation	[3]28	7	6	7	9	9	10
Average temperature	[3]28	13.8	15.7	27.1	41.3	54.2	64.1
Average maximum temperature	[4] 8	27.9	27.9	37.9	53.0	70.1	79.6
Highest temperature	[3]28	50	68	74	85	103	102
Average minimum temperature	[4] 8	6.5	5.2	16.7	28.4	40.6	51.9
Lowest temperature	[3]28	−37	−40	−36	− 3	20	28

	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Mean precipitation, inches	3.66	3.61	3.61	2.43	1.93	1.39	30.18
Average number of days with 0.01 or more inches of precipitation	10	8	9	8	8	7	98
Average temperature	69.1	62.0	58.4	46.8	33.0	19.8	42.1
Average maximum temperature	85.6	81.6	73.0	59.2	42.1	29.4	55.6
Highest temperature	104	99	101	89	72	60	104
Average minimum temperature	56.3	52.3	46.5	34.3	23.2	10.7	31.0
Lowest temperature	35	33	20	4	−2	−26	−40

[1]From Weather Bureau data., U. S. Department of Agriculture. Temperature in degrees Fahrenheit.
[2]1912 to 1938.   [3]1911 to 1938.   [4]1931 to 1938.

moderately warm summers. Mean annual temperature for the period 1911 to 1938, inclusive, is 42.1°F. The maximum temperature listed is 104°F. and the minimum for this period is -40°F. The average length of growing season is 122 days, with the average date of last killing frost in the spring being May 25 and average date of first killing frost in the autumn being September 24. Since climate is one of the outstanding factors in determining success or failure of forest plantings and seedings, pertinent data are given in Table 1. During each of the critical months of June to September, inclusive, there are usually at least 3 to 4 effective rains of 0.5 inch or over in normal years but in years of extreme drought this may average only one effective rain per month.

The topography of the study area is slightly undulating and the soils are generally deep droughty outwash sands, usually submarginal in character for agricultural use. They were mapped by the U. S. Bureau of Chemistry and Soils as Plainfield sands and fine sands.

The forest cover on these soils was formerly largely red pine (*Pinus resinosa* Ait.) with some eastern white pine (*Pinus strobus* L.), and jack pine (*Pinus banksiana* Lamb.) in various mixtures depending on variations in soil texture, fertility, and water relations.

The original forest was removed by logging from 20 to 40 years ago and the remaining cover in most places has little or no resemblance to a well-managed forest. The condition has been aggravated by re-peated forest fires which have swept over the residual stand, resulting in a present cover of open grassland, or, in some places, poor stands of quaking aspen (*Populus tremuloides* Michx.), large-tooth aspen (*Populus grandidentata* Michx.), pin cherry (*Prunus pennsylvanica* L. and P.), and northern pin oak (*Quercus ellipsoidalis* E. J. Hill). The fires caused a deterioration of site and, due to the slow processes of natural restoration, the best solution in changing this land from a nonproductive liability to a national asset is reforestation by planting or direct seeding of species which are adapted to these sites, such as jack pine and red pine.

A portion of the area has shallow ground-water within 10 feet of the surface. In small localized areas the water table is within 2 to 5 feet of the surface and the capillary rise in such areas is sufficient to make initial planting and direct seeding considerably easier, not only because such sites are less droughty, but because of decreased probability of heat injury to small seedlings.

A mechanical and chemical analysis of the soil in the two extremes of topography in one of the study areas is given in Table 2. In addition to the analyses shown, a test for total nitrogen was run for the top 6 inches in each of the two sites and these tests showed 0.058 and 0.050 percent, respectively, for upland and lowland. Inspection of Table 2 indicates there was not much difference in the two extremes of soil conditions. The main difference is a somewhat lower fertility in the ground-water podsol area, referred to in the table as lowland, and slightly more silt and clay in the top 6 inches than in the upland site.

FIELD PLANTING EXPERIMENTS

In the spring of 1937 a 3.3-acre plot was planted to 1,000 trees each of 6 different age classes, namely:

TABLE 2. Mechanical and chemical analysis of soil.

Site	Depth in inches	pH[1]	Percent of silt plus clay[2]	Moisture equivalent	Wilting coefficient[3]	Available pounds per acre per 7 inches[4]			
						Phosphorus	Potassium	Calcium	Magnesium
Upland with water table at depth of 10-12 feet	0–6	6.0	9.0	4.05	2.20	90	320	500	300
	6–12	6.0	9.0	2.29	1.24	25	104	500	275
	12–18	6.0	6.0	1.71	0.93	25	240	500	275
Average	0–18	6.0	8.0	2.68	1.44	47	221	500	283
Lowland with water table at depth of 2-4 feet	0–6	6.0	15.0	6.48	3.52	26	196	500	325
	6–12	6.0	6.0	2.78	1.51	25	168	500	300
	12–18	6.0	5.0	1.78	0.97	25	128	500	300
Average	0–18	6.0	8.7	3.68	2.00	25	164	500	308

[1]La Motte - Kenny.
[2]Bouyoucos hydrometer.
[3]Computed from formula: Wilting coefficient $= \dfrac{Moisture\ equivalent.}{1.84}$
[4]Hellige-Truog field test kit.

TABLE 3. Influence of shallow water table on survival of several age classes of conifer planting stock, with the first season occurring in a severe drought year. Planted, spring 1937.

Species	Age class	Field survival at end of 1st, 2nd, 3rd, and 4th growing seasons				
		UPLAND[1]				
		1 (1937)	2 (1938)	3 (1939)	4 (1940)	Basis, number of trees
		Percent	Percent	Percent	Percent	
Jack pine	1–0	29.2	22.3	22.3	22.3	661
	2–0	29.8	21.8	21.8	21.7	674
	1–1	33.2	28.3	27.7	27.6	693
Red pine	2–0	14.5	7.7	7.6	7.6	692
	2–1	16.1	9.2	9.2	9.2	683
	2–2	45.1	27.8	27.5	27.5	636

Species	Age class	Field survival at end of 1st, 2nd, 3rd, and 4th growing seasons				
		SUBIRRIGATED[2]				
		1 (1937)	2 (1938)	3 (1939)	4 (1940)	Basis, number of trees
		Percent	Percent	Percent	Percent	
Jack pine	1–0	76.8	71.4	71.4	71.4	339
	2–0	81.3	80.0	80.0	79.8	326
	1–1	82.4	80.1	79.1	79.0	307
Red pine	2–0	64.3	58.4	58.4	58.3	308
	2–1	71.3	63.4	61.8	61.8	317
	2–2	84.9	79.4	79.1	78.9	364

[1]Water table mostly at 8 to 12 feet.
[2]Water table at 3 to 6 feet.

2-0, 2-1, and 2-2 red pine and 1-0, 2-0, and 1-1 jack pine.[3]

There were 100 trees of each species planted in 10 replications of each age class. About 35 percent of the planting area had a water table within 3 to 6 feet of the surface, while on the remainder of the plot the water table was at a depth of 6 to 12 feet. The furrows in which the planting was done were plowed at approximately right angles to the contour of the land.

EFFECT OF SHALLOW WATER TABLE

During the period 1937 to 1940, inclusive, survival counts and measurements of growth were made each fall on the various classes of stock. Survival was from 3 to 8 times as high in the ground-water podsol area as in the upland area (Table 3). The difference in survival between upland and lowland was found to be highly significant statistically when compared by analysis of variance.

This striking difference was attributed largely to

[3] The various figures, such as 2-0, 2-1, 2-2, refer to the age and class of planting stock. The first figure refers to the number of years the plant was grown in the seed bed and the last figure refers to the number of years grown in the transplant bed. Thus, a 2-0 tree is grown two years as a seedling but is not transferred to a transplant bed to develop a better root system. A 2-1 tree is grown two years in the seed bed and one year in the transplant bed.

the higher percentage of available soil moisture within rooting depth of the trees in the area having the water table within 3 to 6 feet of the surface. The value of the test was enhanced because 1937 was the most severe drought year on record in this vicinity; the rainfall for 5 consecutive months, from May 1 to Sept. 30, was only 5.93 inches and averaged 34 percent of normal. The drought was not broken until early October. Precipitation and soil moisture data for 1937 for the two sites are given in Figure 1. Soil moisture samples were taken in three 6-inch levels from four vertical-walled profiles dug in each of the two sites on every occasion of sampling. The data are averaged for the 0- to 18-inch average rooting depth.

Moisture relations for the growing season as a whole were better in the lowland than in the upland area, although the minimum reading was obtained on August 25 in the lowland area.[4] This was due no doubt to the fact that the water table in late summer of 1937 had dropped to 6 feet below the surface, and hence the capillary contact with the surface soil was temporarily broken. In most years the water table is only 3 to 4 feet below the surface on the lowland areas.

Since losses due to drought are a function of its duration as well as its intensity, the trees in the lowland area survived much better. The available soil moisture was below 2.5 percent for 31 consecutive days while in the upland area it was below 2.5 percent for fully 64 days.

Close observation showed that there was practically no mortality on the upland area at the end of July, but it was beginning to show up rather strongly by the middle of August, with severe losses by the end of that month. In other words, severe losses occurred when the available soil moisture within the rooting depth of the plants (18 inches) had dropped below 2.5 percent available moisture for 40 consecutive days and where no effective rain of one-half inch or more had fallen for about 60 days. It is of further significance to state that when the soil moisture data were plotted separately for 0 to 6, 6 to 12, and 12 to 18 inch depths, it was found that available soil moisture in the 12 to 18 inch zone of the lowland area dropped below 2 percent for only 4 days during the entire summer. On the uplands it was below that value for 32 consecutive days in late July and early August, on one occasion, and for 17 consecutive days in the latter part of August and the first part of September.

First-year losses in 1937 in the upland sand plains are therefore attributed largely to prolonged drought. A study of the temperature records for 1937 showed that year to be only slightly above normal for the summer months, and, moreover, examination of the

[4] The term "available moisture" as used in this study refers to the difference between the percentage of total moisture in the soil and the wilting coefficient. The latter was determined from the formula, wilting coefficient = $\dfrac{\text{moisture equivalent}}{1.84}$. Observations with potted plants indicate that the wilting percentage for sandy soils is quite close to that obtained by the formula.
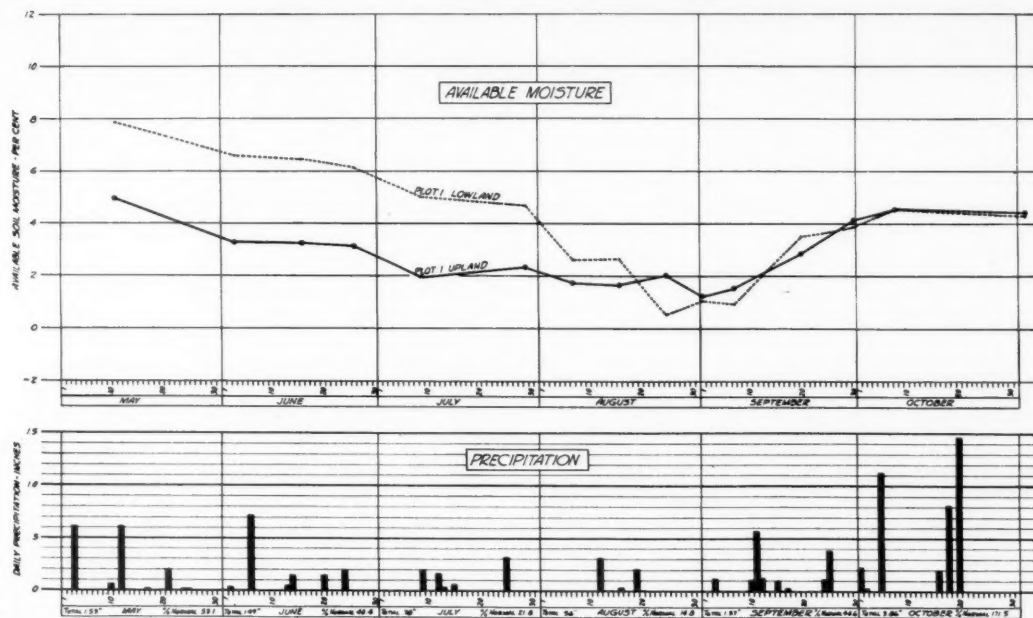
FIG. 1. Precipitation and average available soil moisture for 0- to 18-inch depth for Plot 1, Nicolet National Forest, Wisconsin, 1937. The lowland portion of the plot had a permanent water table within 4 to 6 feet of the surface.

trees at time of making survival counts in late autumn showed no heat lesions on the stems.[5]

The causes of tree losses in the study area are listed in Table 4. Drought caused most of the loss but it will be noted that there is considerable mortality due to larvae of May beetles (*Phyllophaga* sp.) depending on closeness of water table. The only explanations found to date are that the generally higher moisture content and lower soil temperatures make the subirrigated areas a rather poor medium in which eggs of the insect can hatch. Also, it is believed that the ground-water podsol areas are comparatively unfavorable for overwintering of the larvae of the May beetles, which in their attempt to burrow deeply enough to get below the frost line would encounter the nearly saturated capillary fringe which lies just above the water table.

In the autumn of 1938 separate counts were made on this field planting area based on 20 subplots, each containing 20 trees on the same contour level. Twenty of these subplots were obtained for each of the six age classes of stock used. In each case depth to water table was determined by boring a hole with a post-hole auger and using a measuring stick and flashlight to get the readings. The data were then

segregated into nine classes, depending on depth to water table.

These values for the red pine and jack pine are presented graphically in Figures 2 and 3, respectively. The depths to water table are not, however, those which occurred in the late autumn of 1938 but rather are the readings which prevailed in the summer and autumn of 1937 when the water table was 2.8 feet lower than in the autumn of 1938. This basis is considered most equitable because the largest portion of the mortality occurred in the late summer of 1937 and it was the depth of the water table at that critical time which was the important reason for differences in survival.

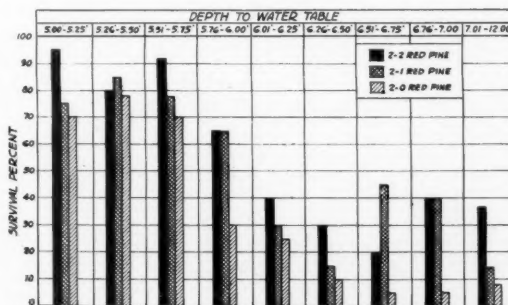The data for red pine in Figure 2 generally show

FIG. 2. Effect of depth to water table on survival of red pine at the end of the second season's growth. Mountain, Wisconsin. 1938.

a gradual reduction in survival as the depth to water table increases, with the sharpest reduction occurring where the water table dropped below 6 feet. It will also be noted that the oldest age class

TABLE 4. Causes of mortality in field test plots planted in spring 1937, Nicolet National Forest.

Year	Species	Age class	Mortality of planted trees due to various causes			
			UPLAND			
			Drought	May beetle Larvae	Other[1]	Total
			Percent	*Percent*	*Percent*	*Percent*
1937	Jack pine	1-0	37.1	19.5	14.2	70.8
		2-0	33.7	27.0	9.5	70.2
		1-1	37.1	23.9	5.8	66.8
	Red pine	2-0	45.8	28.7	11.0	85.5
		2-1	46.3	32.6	5.0	83.9
		2-2	22.8	31.5	0.6	54.9
1938	Jack pine	1-0	0.0	1.1	5.8	6.9
		2-0	0.0	1.6	6.4	8.0
		1-1	0.0	0.6	4.3	4.9
	Red pine	2-0	0.0	1.6	5.2	6.8
		2-1	0.0	2.8	4.1	6.9
		2-2	0.0	9.8	7.5	17.3
1939 and 1940	Jack pine	1-0	0.0	0.0	0.0	0.0
		2-0	0.0	0.0	0.1	0.1
		1-1	0.0	0.0	0.7	0.7
	Red pine	2-0	0.0	0.0	0.1	0.1
		2-1	0.0	0.0	0.0	0.0
		2-2	0.0	0.0	0.3	0.3

Year	Species	Age class	Mortality of planted trees due to various causes			
			SUBIRRIGATED			
			Drought	May beetle Larvae	Other[1]	Total
			Percent	*Percent*	*Percent*	*Percent*
1937	Jack pine	1-0	9.1	4.7	9.4	23.2
		2-0	8.3	5.2	5.2	18.7
		1-1	7.8	5.2	4.6	17.6
	Red pine	2-0	16.6	12.3	6.8	35.7
		2-1	17.7	6.6	4.4	28.7
		2-2	9.1	6.0	0.0	15.1
1938	Jack pine	1-0	0.0	0.3	5.1	5.4
		2-0	0.0	0.3	1.0	1.3
		1-1	0.0	1.0	1.3	2.3
	Red pine	2-0	0.0	0.6	5.3	5.9
		2-1	0.0	0.9	7.0	7.9
		2-2	0.0	3.3	2.2	5.5
1939 and 1940	Jack pine	1-0	0.0	0.0	0.0	0.0
		2-0	0.0	0.0	0.2	0.2
		1-1	0.0	0.0	1.1	1.1
	Red pine	2-0	0.0	0.0	0.0	0.0
		2-1	0.0	0.0	1.6	1.6
		2-2	0.0	0.0	0.5	0.5

[1]Losses listed as "other" include mostly unclassified causes of death; a few trees which died due to poor planting and nematodes are included in this category.

of planting stock usually has the highest survival.

The data for jack pine in Figure 3 show the same general trend as for red pine, with the exception of a few bars in the 6.5- to 7.0-foot depth. These variations are probably due to comparatively meager data for that portion of the bar chart or are due to local variation in soil or cover. The bars for the 1-0 jack pine show the most uniformly smooth trend. Considering the averages for all age classes of jack pine, the sharpest break occurs where the water table drops below 6.25 feet.
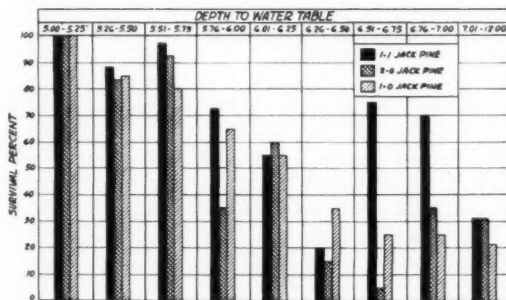

FIG. 3. Effect of depth to water table on survival of jack pine at the end of the second season's growth. Mountain, Wisconsin. 1938.

The reasons why the survivals dropped off rather sharply at a water table depth of 6.00 to 6.25 feet and why the 2-2 red pine showed the best first-year survival were believed to be related largely to the root habit of the plants. To check the validity of this assumption, 24 trees on the upland portion of the study plot (4 trees of each age class) were carefully excavated and drawn to scale on cross-section paper.

The summarized data on correlation of first year survival and rooting depth are shown in Figure 4,
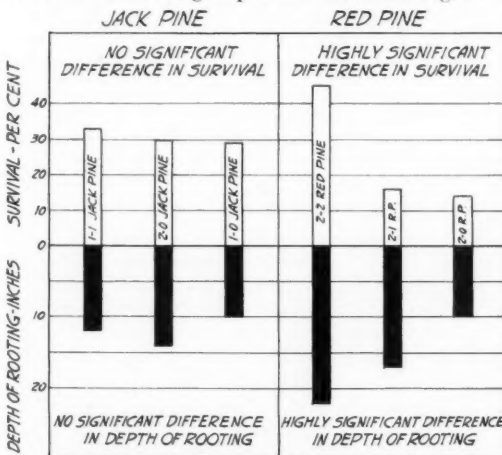

FIG. 4. Relationship of survival to depth of rooting at the end of the first growing season on a droughty loamy fine sand. Nicolet National Forest, Wisconsin, 1937.

which indicates an average rooting depth of 22 inches for the 2-2 red pine and a correspondingly higher survival. The data were compared statistically by analysis of variance, which showed that the 2-2 red pine rooting depth was significantly higher than the other age classes within that species, while within the jack pine age classes there was no significant difference in survival or rooting depth.

In comparing species, however, it will be seen that jack pine of an age and size comparable to red pine invariably shows higher field survival.

Measurements of the six kinds of stock used in the test and taken at time of planting are given in Table 5. The 2-2 red pine was very much larger than any

TABLE 5. Measurements of nursery stock planted on study area in May, 1937.

Species	Age class	Basis, number trees measured	Average length in inches		Average diameter of stem (64ths inch)
			Tops	Roots	
Jack pine....	1-0	50	[1]2.2±0.51	6.9±1.31	6±1.08
Jack pine....	2-0	50	3.7±0.75	8.7±0.91	5±1.52
Jack pine....	1-1	50	3.3±0.67	12.7±1.80	8±1.34
Red pine.....	2-0	30	2.2±0.49	9.2±2.29	5±1.40
Red pine.....	2-1	50	4.5±0.14	10.6±1.57	8±1.28
Red pine.....	2-2	50	8.7±2.39	11.4±1.88	13±3.31

Species	Age class	Basis, number trees measured	Average green weight in grams			Average top-root ratio[2]
			Total	Tops	Roots	
Jack pine....	1-0	50	0.88±0.32	0.62	0.26	2.42:1
Jack pine....	2-0	50	1.41±0.78	1.14	0.26	4.33:1
Jack pine....	1-1	50	4.91±2.22	3.44	1.48	2.33:1
Red pine....	2-0	30	2.18±1.37	1.67	0.51	3.27:1
Red pine....	2-1	50	4.41±2.21	2.89	1.52	1.90:1
Red pine....	2-2	50	22.39±13.44	18.76	3.63	5.16:1

[1]Values show standard deviation.
[2]Based on total top weight divided by total root weight, and with weight values carried out to 3 places beyond decimal point.

of the other 5 classes and, if these remaining 5 lots are considered in terms of survival and rooting depth, one must conclude that jack pine has more inherent drought hardiness because the 3 lots of jack pine have an average survival on the upland of 30.7 percent as compared with 15.3 percent for the two smaller age classes of red pine.

Survival data on this study area were also taken in 1938, 1939, and 1940, which revealed some interesting points. Precipitation during the year 1938 was quite favorable, being about normal on the study plot for all months from May to October, inclusive. The heavy snowfall in the winter of 1937-1938 and the heavy rains of the spring of 1938 also were effective in raising water levels by fully 2 feet and the relatively high water table was maintained all through 1938 as illustrated by Figure 5.

By referring again to Table 3, it will be noted that there was much less mortality in the second year (1938) than in 1937. This was due largely to the fact that the plants were somewhat better established and in addition had a much more favorable growing season. Losses in the third and fourth year were negligible.

The soil moisture data for the upland and lowland areas of the study plot are given in Figure 6 for 12 different sampling periods between April 16 and September 28, 1938. The samples taken to a depth of 24 inches by 6-inch layers showed that the amount of available moisture in the lowland area increased markedly with an increase in depth of sampling. This trend is, of course, logical because, with the 2-foot rise in water table between the autumn of 1937 and the spring of 1938, the water table in the subirrigated lowland was at an average depth of 2 to 4 feet, and, in sampling the various soil levels, some of the moisture in the soil samples came from below due to capillary rise. The graphs for the upland portion of the plot, where the water table was between 6 and 10 feet below the surface in 1938, show
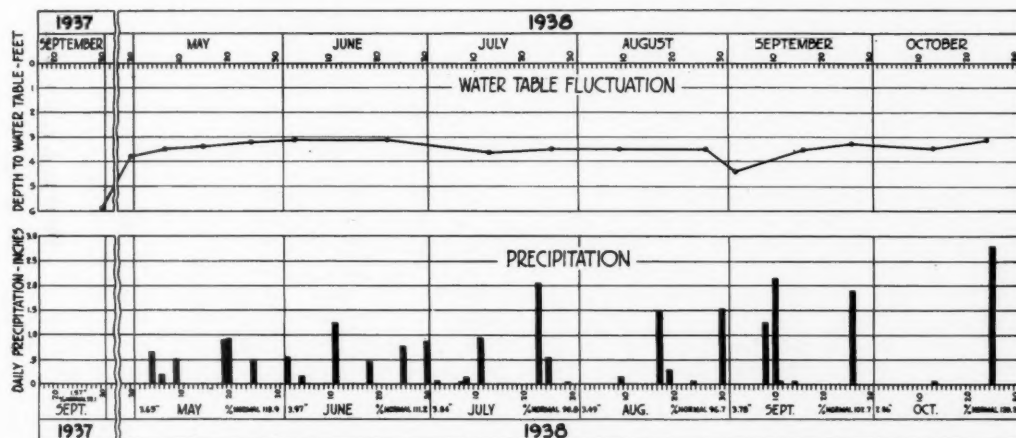

FIG. 5. Fluctuation of water table depth at one sampling station on study area and precipitation for the summer season of 1938. The precipitation record is in striking contrast with the drought year of 1937 given in Figure 1.

rather low soil moisture content in the top 6 inches of soil where the drain caused by roots and by evaporation is greatest in midsummer, and the highest moisture content in the 6- to 12-inch zone.
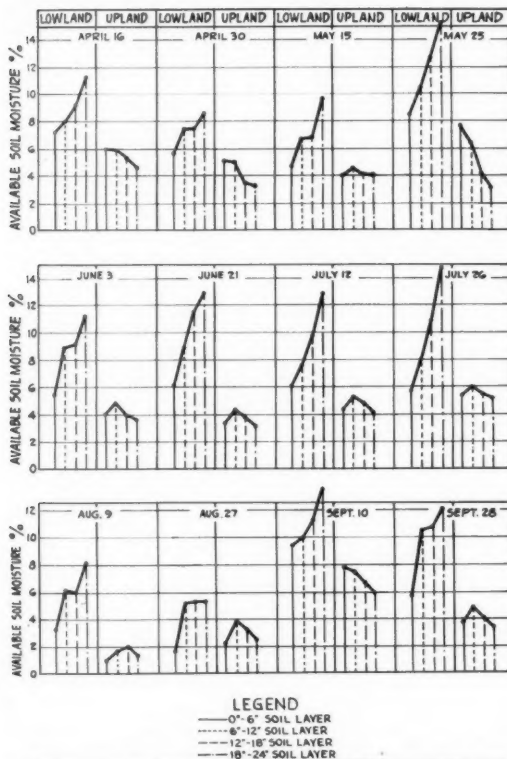

Fig. 6. Available soil moisture percentage obtained by periodic sampling of the study area during the summer of 1938. Plot 1, Nicolet National Forest, Wisconsin.

The graph shows that there was invariably from 3 to 4 percent more available moisture in the lowland than in the upland portions of the plot. Also, it will be noted that only on one occasion did the average available moisture content drop below 2.5 percent, and judging by the rainfall bar chart in Figure 5 its duration could not have been more than 4 or 5 days. This is in striking contrast with the data shown for the year 1937 given in Figure 1, when the available moisture percentage for the rooting depth of the plants was below 2.5 percent for 64 consecutive days in the upland and 31 consecutive days for the lowland.

Survival in Years of Normal Precipitation

It becomes apparent that other factors being favorable, available soil moisture as influenced by water table, and amount and distribution of rainfall are among the principal factors in ability of species to establish and maintain themselves. To support this contention, data are presented on the survivals obtained on an experimental forest plantation established in the fall of 1937 on a site practically identical to the upland portions of the study plot under discussion. First-year survivals recorded in the fall of 1938 were: 1-0 jack pine, 84.7 percent; 2-0 jack pine, 96.6 percent; 1-1 jack pine, 97.0 percent; 1-2 jack pine, 97.4 percent; 1-2 red pine, 97.4 percent; 2-2 red pine, 94.5 percent; 2-1 Scotch pine (*Pinus sylvestris* L.), 98.7 percent. These values for a season with 104 percent of normal rainfall for May 1 to September 30 are in decided contrast with first-year survivals listed in Table 3 for the upland soil in the 1937 drought. The table shows an average survival of only 28 percent for the six age classes listed.

The average available soil moisture percentages for the first growing season (1938) on the autumn of 1937 planting for the top 18 inches of soil were as follows:

May 5.26
June 5.22
July 3.73
August 2.94
September 7.50

Soil moisture samplings were taken twice a month and the lowest available moisture was found to be 2.42 percent on August 9. The average for the 10 values is 4.93 percent. This is considerably more available moisture than the average of 2.7 percent for the 5 months of 1937 shown in Figure 1. These moisture differences in different seasons may not appear large but, when interpreted in terms of capillary tension for a soil of this type (medium sand), the reason for contrast in survival is very obvious. A medium sand with 5 percent of available moisture offers very little opposition to extraction of water by a plant, but when this drops to 1.5 or 2.0 percent the force opposing extraction of water is from 6 to 7 times as great as at 5 percent available moisture.

Growth Rate on Upland and on Subirrigated Sites

Height measurements were taken on approximately 10 percent of the trees on the two types of sites at the end of each of four growing seasons, and are summarized in Table 6. It will be seen that there was usually a slight advantage in height for the subirrigated portion of the plot and for the larger age classes in the case of red pine. Jack pine generally shows a growth rate about double that of red pine.

A further study on effect of subirrigation on a 5-year-old plantation of 1-0 jack pine on a site similar to the experimental plot showed large differences in height growth only where the water table was within 3 feet of the surface, the average tree height being 3.6 feet as compared with 2.6 feet for the remaining areas where the water table ranged from 3 to 10 feet. The data are based on measurements of 839 trees on 31 small sampling plots containing approximately 25 trees each.

TABLE 6. Total height of several age classes of trees planted in the spring, 1937.

| Age class | Height in inches at end of consecutive growing seasons | | | | | | | |
| | Upland site | | | | Subirrigated site | | | |
	1	2	3	4	1	2	3	4
	JACK PINE							
1 – 0......	3	11	24	43	4	12	26	46
2 – 0......	6	11	23	41	6	14	25	50
1 – 1......	5	12	26	44	6	15	31	48
	RED PINE							
2 – 0......	4	6	11	17	4	7	11	19
2 – 1......	5	7	11	20	5	8	14	20
2 – 2......	11	13	17	27	11	13	20	31

EFFECT OF ASPEN OVERSTORY IN DROUGHT YEARS

In 1936 a severe widespread drought, accompanied by heat, practically wiped out thousands of acres of recent forest plantations in the entire Lake States region. Forest officers noted that the damage was much more severe in open areas than in places where some overstory of aspen, scrub oak, or brush was present. The difference was attributed largely to the reduction of heat and drought losses in the shaded areas.

In 1937 a more severe drought, but with near-normal temperatures, occurred in a limited area in the southern part of the Nicolet National Forest. The results from two adjoining plots gave an excellent opportunity to collect comparative data on the beneficial effect of shade provided by a light canopy of aspen. The aspen stand, 15 to 20 feet in height, reduced light intensity to 75 percent of full sunlight at a height of 4.5 feet and to 56 percent at 0.5 feet above ground, with some of the latter reduction caused by a medium cover of bracken fern. The light data are based on 180 readings at each of two heights, using a Weston exposure meter. Measurements were taken in midsummer of the first growing season. The area had been prepared with a heavy Killefer plow in the summer of 1936, and this opened up the stand considerably by plowing out or pushing over by the treads of the heavy tractor about 70 percent of the initial stand. This degree of opening of the canopy was in the nature of a pre-planting release of the overtopping canopy of aspen and paper birch.

A stand table made in the area during the season following plowing showed 1,288 trees per acre distributed as follows: quaking and large-tooth aspens, 853; paper birch, *Betula papyrifera* Marshall, 108; pin cherry, *Prunus pennsylvanica* L., 71; northern pin oak, 32; red maple, *Acer rubrum* L., 224. The extreme range of diameters at breast height was 0.5 to 4.0 inches, but over 95 percent of the trees were in either the 1- or 2-inch class. The soil was a medium sand which differed very little in mechanical and chemical analysis from the nearby plot planted

in the open area referred to in Table 3. The plot consisted of five replications of 200 trees of each of six age classes and the differences in survival between comparable age classes or two types of sites, given in Table 7, were highly significant statistically when tested by analysis of variance.

TABLE 7. Influence of a light aspen overstory on survival of forest plantings in a drought year.

| Age class of stock | First-year survival percentages[1] | |
	Open	Aspen cover
	JACK PINE	
1 – 0.................	29.2	68.9
2 – 0.................	29.8	78.6
1 – 1.................	33.2	83.4
	RED PINE	
2 – 0.................	14.5	63.7
2 – 1.................	16.1	68.6
2 – 2.................	45.1	80.8

[1] Data for open areas based on 600 to 700 trees in each age class. Under aspen cover data are based on 800 trees of each age class.

In reforestation work in the Lake States, about 1,000 trees are planted per acre and the plantation should not be considered successful unless there are about 500 to 600 surviving trees present per acre. Using this as a criterion, it will be seen that for each age class involved, the overhead cover made the difference between success and failure.

Soil moisture samples taken by 6-inch levels to a depth of 18 inches in the aspen plot showed that it was generally and rather consistently lower in available moisture by about one percent than open upland sites referred to in Figure 1. This indicates that the roots of the aspen and paper birch created a heavier drain on soil moisture than the blue grass, timothy, and sedge cover of the upland part of plot 1 shown in Figure 1. Therefore, the difference in survival could not be attributed to any conservation of soil moisture by the aspen cover.

The difference in survival was attributed to a marked reduction in evaporation by the aspen overstory. Two Bates' evaporimeters, placed on the ground in each of the two types of conditions, showed a tremendous reduction in evaporation under the aspen (Figure 7). It is seen that the evaporation stress is generally from 6 to 10 times as great in the open during the summer months. This difference can be considered as a composite effect of reduction of wind velocity, solar radiation, temperature, and saturation deficit, and since these factors intimately affect transpiration it is evident that transpiration stresses must have been much less severe under the aspen.

It is of interest to note that evaporation in the aspen was greater in the middle of May than during most of the summer. This is attributed to the fact that the leaves were very small at that time and they were not fully developed until mid-June.

The comparative drought losses in the two types of sites during the first season after planting are

given in Table 8. A very heavy loss was sustained in both species in the open type of site, with losses running from 4 to 6 times as great as in the aspen cover. Red pine had greater losses than jack pine in all cases where stock of the same size was compared. In June 1939 the plot was given a low release
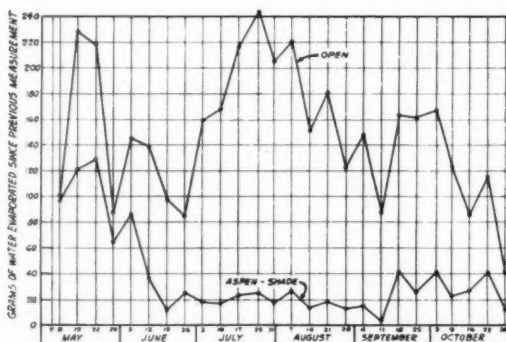

FIG. 7. Comparative loss from Bates' evaporimeters in open and under a light canopy of 20-foot-high overstory of aspen and paper birch and a medium ground cover of bracken fern.

from birch and other herbaceous competition, and part of it received a high release which caused no appreciable response the following season.

Survivals at the end of 4 years under aspen for the six age classes listed in Table 7 are:

	Percent
1-0 jack pine	51.7
2-0 jack pine	64.3
1-1 jack pine	74.8
2-0 red pine	50.3
2-1 red pine	50.4
2-2 red pine	74.3

The fourth-year survival of these age classes on upland sites devoid of cover is shown in Table 3.

TABLE 8. Comparative drought losses in 1937 in open sites and under light aspen shade.

Age class	First-year mortality percentages	
	In open	In aspen cover
JACK PINE		
1 – 0	37.1	7.3
2 – 0	33.7	6.1
1 – 1	37.1	5.0
Average	36.0	6.1
RED PINE		
2 – 0	45.8	12.4
2 – 1	46.3	9.4
2 – 2	22.8	6.2
Average	38.3	9.3

The average heights in inches of the six age classes grown under aspen overstory at end of four years are 25, 28, 36, 10, 12, and 21, respectively. A comparison with heights of the same age classes grown entirely in the open (Table 6) reveals that the jack

pine was 44 percent higher in the open than in shade, while red pine was 49 percent higher in the open. This leads to the conclusion that although partial cover had a favorable influence on initial survival, it had a definite effect in reducing height growth.[6]

ROOT DEVELOPMENT AND DROUGHT RESISTANCE

At the end of the first and second growing season in the field, roots of 56 trees on the study plots were carefully exposed, drawn to scale, and photographed. These studies revealed some interesting facts as regards the rooting habits of the various age classes and species in this locality. They showed that in the first year after field planting the root growth is almost entirely downward, while in the second year there is considerable development of lateral roots, as illustrated by Figures 8 and 9.[7] The data also revealed that jack pine quickly developed a widespreading root system and to this is attributed its greater drought resistance.

A third point brought out by the root studies is the fact that in these extremely sandy soils, slit planting appeared to have little or no adverse influence on root development attained by the end of the second year of 1-0, 2-0, or 1-1 jack pine, or 2-0 or 2-1 red pine.

It should be explained here that in reforestation work in the Lake States two common methods of planting are used—one known as slit planting and the other as center-hole planting. In the former method, a steel planting bar with a blade 3 inches wide and 11 inches long is thrust vertically into the ground and manipulated so as to leave a slit in the ground 3 inches long and about 1 inch wide, made to the full depth of the planting bar. The slit direction is made, in the case of planting in furrows, at right angles to the furrow direction as is illustrated by the black line in Figure 10B. The two double parallel lines in the figure represent the edge of the furrow, which in this case was 1 foot wide. The newer type of furrowing equipment now available plows furrows from 24 to 30 inches wide and is consequently more effective in reducing first-year competition from vegetation such as sod and brush.

In planting trees by the bar method, the man who makes the slit also plants the tree by holding it with two fingers against or near one end of the slit and closing the slit by reinserting the bar into the soil about 2 inches from the slit, forcing the bar forward to close the hole and, as a final step, tamps the soil with his heel. With the center-hole method, a hole from 4 to 6 inches in diameter is dug with a mat-

<div style="font-size:small">

[a] To counteract this adverse effect on growth it has become standard practice in national forest conifer plantations in the Lake States to remove part of the overstory in the form of repeated release cuttings performed usually in the second, fourth, and sometimes sixth year after planting. In any one operation from 50 to 80 percent of the existing stems are cut or girdled.
[7] In Figures 8 and 9 it will be noted that first-year depth of root penetration is not as great as indicated by Figure 4. This difference is accounted for by the fact that the first-year trees shown in Figures 8 and 9 were taken from a plot planted in the autumn of 1937, followed by a season of normal rainfall, while the trees on which Figure 4 is based were planted in the spring 1937 and were subjected to a severe drought which probably caused the plants to root deeply.

</div>

tock or spade and loose soil is packed around the tree, which is planted in the center of the hole. The 2-2 red pine stock used in this experiment was planted by the center-hole method.
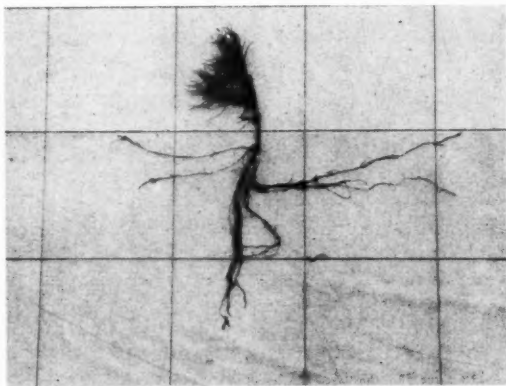
The second-year root development of jack pine as demonstrated by Figures 10 and 11 is in striking contrast to that of red pine (Figures 9 and 12), especially when the original size of the stock at time of planting (Table 5) is considered. This root-extension ability is undoubtedly one of the reasons why jack pine is more drought hardy than red pine, and, in fact, is classified as the best species for droughty and impoverished sand plains in the Lake States. The selection of this species for such sites hinges not only on drought resistance but also on its ability to thrive on soils very low in available nutrients, as has been demonstrated by Wilde (1938).

Figures 10 and 11 show root development of 2-0

and 1-0 jack pine on two different types of planting sites—one subirrigated, the other upland. The trees made extensive lateral root growth, practically all of which occurred the second year. The lateral roots were especially well developed in the top 4 to 6 inches of soil on the upland site, and in both cases showed more growth in and parallel to the furrow than at right angles to it, the maximum spread in

A
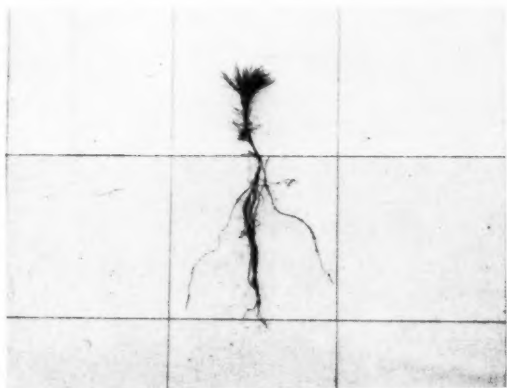
A

B

FIG. 8. Root development of 1-0 jack pine planted in upland portions of study areas. *A*. Development at the end of the first growing season in the field. *B*. Development at end of the second growing season. Both trees planted by the bar-slit method. Views show root development parallel with bar-slit plane and at right angles to furrow direction. (Background composed of 1-foot squares.)
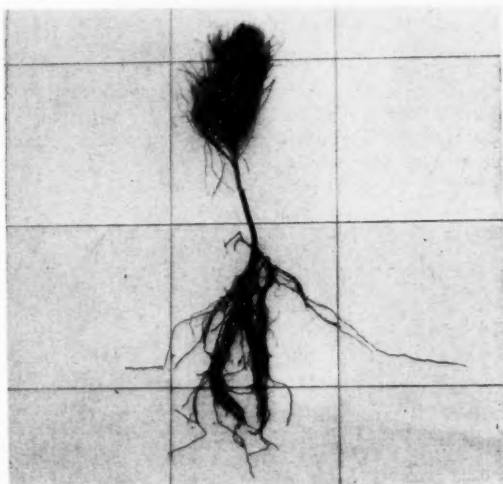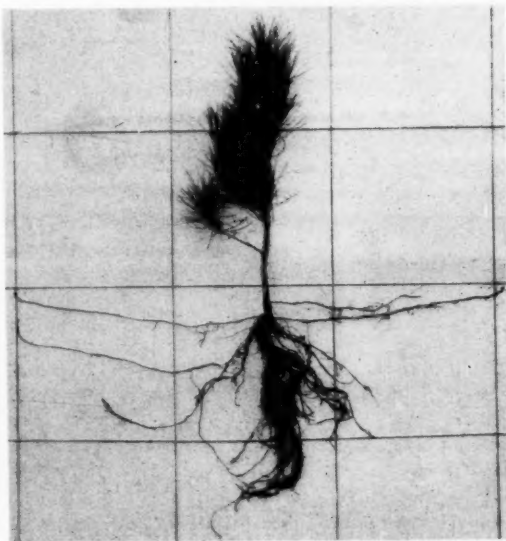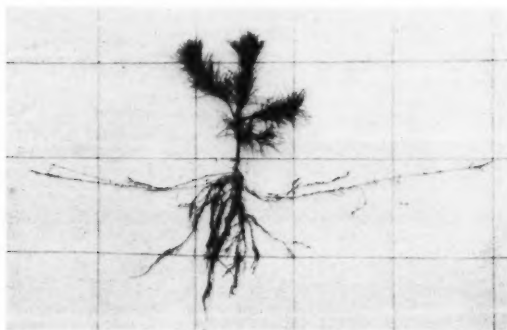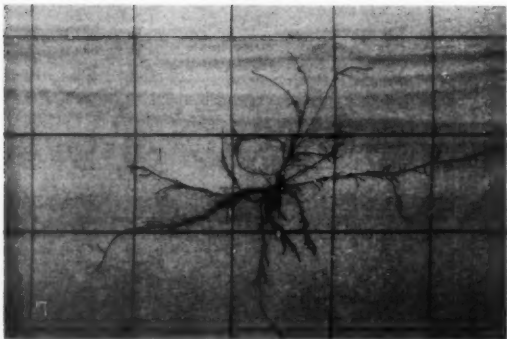

B

FIG. 9. Root development of 2-2 red pine planted in the upland portions of the study areas. *A*. Development at the end of the first growing season in the field. *B*. Development at end of the second growing season. Both trees planted by the center-hole method, with spades. Views show development at right angles to furrow direction. (Background is of 1-foot squares.)

furrows being 1.5 to 2.0 times that at right angles to the furrows. This can be attributed to a reduction of competition for moisture effected by the plowing of the furrow and removal of the dense sedge and grass sod which was present between the furrows.

It may be concluded from the root studies that there was not very much difference at the end of the second year in rooting habits of the plants in the two types of planting sites—upland or lowland—although this is more than likely to occur in future years because of the limited rooting depth in the subirrigated areas. There was some tendency for the plants in the subirrigated area to have somewhat more lateral spread and less rooting depth than on the upland. The maximum spread of roots observed in any of the plants was on the moist lowlands where a 2-0 jack pine seedling at the end of the second year after field planting showed a lateral spread of 8.5 feet.

The available information obtained on root studies on this plot is summarized in Table 9.
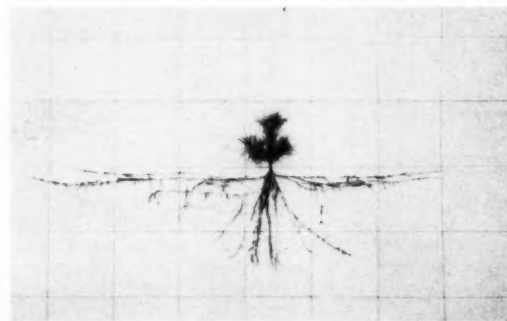
DIRECT SEEDING EXPERIMENTS

As a corollary to the study of effect of various factors on survival of planted trees, several studies

TABLE 9. Comparative root development of red and jack pines in upland and lowland at end of the second growing season in the field.
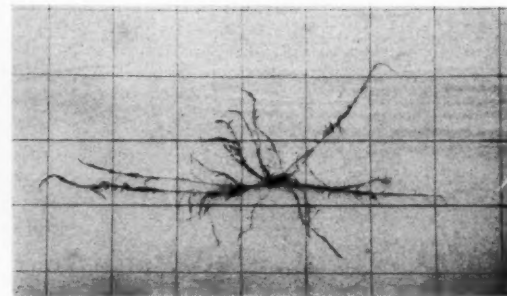
	UPLAND		LOWLAND	
	Jack pine [1]	Red pine [2]	Jack pine [1]	Red pine [2]
Maximum length of Roots parallel to furrow (inches)	45.0	22.0	64.0	22.0
Average maximum (inches)	25.2	16.6	30.0	15.3
Maximum length of Roots at right angles to furrow (inches)	33.0	23.0	58.0	36.0
Average maximum (inches)	25.5	21.6	32.8	15.8
Maximum depth of rooting (inches)	23.0	18.0	23.0	20.0
Average maximum (inches)	19.7	17.3	16.9	15.9
Basis (Number of trees)	4	4	9	9

[1]Based on measurements of 1-0, 2-0, and 1-1 jack pine.
[2]Based on measurements of 2-0, 2-1, and 2-2 red pine.

A

B

FIG. 10. Root development of 2-0 jack pine two years after planting in the lowland (subirrigated) portion of the study area. Tree planted by the bar-slit method. A. Development of roots parallel to furrow direction and at right angles to bar-slit plane. B. Lateral root development of the same tree after top of tree and all roots except laterals were removed. The two double lines indicate furrow direction and width. Black strip under center of tree represents approximate position of bar at time of planting. Permanent water table 4 feet below surface of ground. (Background is composed of 1-foot squares.)


A

B

FIG. 11. Root development of 1-0 jack pine two years after field planting in upland portion of study area. A. Development parallel to furrow direction and at right angles to slit plane. B. Lateral root development after top of tree and all roots except laterals were removed. The two double lines show the direction and approximate width of the furrow. (Background composed of 1-foot squares.)
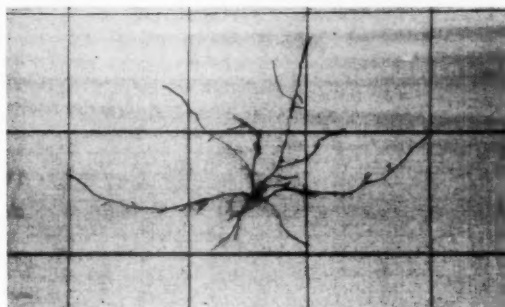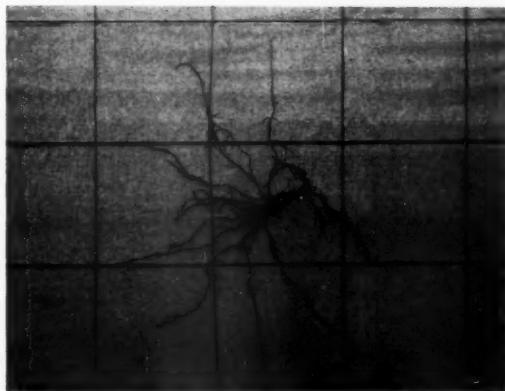
FIG. 12. Lateral development of red pine roots two years after planting. Double lines indicate furrow direction. *A*. 2-0 red pine in lowland (subirrigated) portion of study area, planted by the bar-slit method. *B*. 2-2 red pine in upland portion of study area, planted by the center-hole method. (Background composed of 1-foot squares.)

were made to determine what influence shallow water table might have on direct seeding. Direct seeding of forest species in the United States, and especially in the Lake States, has not been very successful, and this has been variously attributed to the depredations by rodents and birds on the seed, slow initial growth of many forest species, losses due to heat and drought, and inability to compete successfully with ground and overhead cover. On upland soils, seeding has been successful only in years of abundant rainfall, well distributed through the growing season, as has been pointed out by Shirley (1937).

EFFECT OF SHALLOW WATER TABLE ON SURVIVAL IN A DROUGHT YEAR

In the spring of 1937 the administrative officers of the Nicolet National Forest established a 123-acre direct seeding experiment on a typical undulating Plainfield sand soil type very similar to the field planting experimental area described in the first portion of this paper. The seeding plot was only a few miles from the planting plot and hence the

rainfall and other weather data can be considered as being fairly representative of this seeding area.

The seeding was done in the spring of 1937 at weekly intervals from April 9 to June 4 and was accomplished mostly by the aid of hand-operated mechanical seeders of the Planet Jr. type, which is used extensively in garden and nursery work. Two small plots were seeded by hand, broadcasting in furrows. In the mechanically seeded areas the seeder was set so as to feed out a continuous stream of seed into a single drill and the seeder was run down the center of plowed furrows prepared the previous season. In most cases a quarter-pound of seed was used per acre but in a few cases up to one or two pounds of seed were sown per acre.

Good germination had occurred by the middle of July, with an average stocking of 3,000 seedlings per acre. By August 12, of that year, the average stocking had dropped to 1,440 trees per acre, and to 1,160 trees per acre by October 10. Losses were due largely to the prolonged drought of 1937. Distribution of rainfall in this vicinity for 1937 is given in Figure 1 and for 1938 in Figure 5.

A careful examination of the area in 1937 and 1938 showed a very marked difference in stocking, which appeared to be correlated with depth to water table and, of course, with topography. Having previously observed the close correlation of survival of forest plantations with depth to water table, it was decided to extend this same technique of study to the direct seeding experiment.

In October 1938, survival counts were made on 8 of 15 subplots and depth to water table at each of the 76 counting plots was determined.

The results, graphically presented in Figure 13, show a very striking trend in stocking and a high correlation with depth to water table. The graph indicates that for areas where the water table is within 2 to 4 feet of the surface, there is a much higher survival than where the water table is below 4 feet.

The explanation for the sharp break at a depth of between 4 and 5 feet can be correlated with the com-
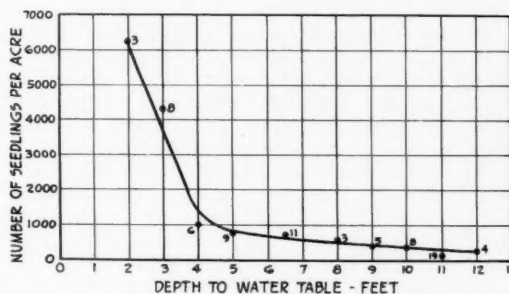

FIG. 13. Survival of jack pine in a direct seeding experiment at the end of the second growing season in the field in relation to depth of water table. All data on basis of one-quarter of pound of seed per acre and survival counts made in the autumn of 1938. Figures opposite each point represent number of plots averaged for that value.

paratively higher moisture content of the top 6 inches of soil, which represents the depth of rooting of 1-year-old jack pine seedlings under these field conditions. In areas where the water table is quite close to the surface, that is, within 2 to 4 feet, capillary moisture from the water table readily rises to the surface. Repeated observations made on these areas at different times of day during the summer months showed that, where the water table was within 2.5 feet, the surface of the soil was invariably moist all through the day, and that where it was from 2.5 to 4.0 feet deep, the surface soil was intermittently moist from capillary rise, depending on time of day and on air temperature, humidity, wind velocity, and other factors which influence evaporation rate. The number of days since the last rain also appeared to influence the time in the morning when the surface of the soil dried out to a depth of one or more inches.

Evidently for direct seeding of jack pine on areas with little or no overhead cover, and where the water table is within 2 to 4 feet of the surface in midsummer, success is reasonably certain even in drought years. It must be kept in mind that the seeding area on which the data for Figure 13 is compiled had gone through the most severe and prolonged drought ever recorded for that part of Wisconsin. The slight downward trend of the curve in Figure 13 for water table depths of 5 to 12 feet must not be considered as a function of depth to water table because, beyond depths of 4 to 5 feet, the water table does not have much significance in first-year survival of pine seeding. For regular planting stock the effect extends to 6 feet. In reality, the plotted average stocking for the 5- to 12-foot range must be considered as an indication of relative topographic position of the sampling areas on the 123-acre plot, which was located on a slightly undulating sand plain, underlain by a water table whose depth of 2 to 12 feet varied almost directly with topography.

Seedlings located on the slopes or tops of the broad knolls naturally were in positions where the wind had more drying power and where soil moisture conditions were least favorable because of exposure and slightly lighter soil texture.

Measurements made on the seedlings indicate that jack pine makes considerable development and is fairly well established in its second year after being direct seeded in the field. These data are given in Table 10, which shows that larger trees were produced in areas where the water table is within 4 feet of the surface, based on oven-dry weight of the plants. The balance of the trees (top-root ratio) is considered exceptionally good for this species.

SOIL TEMPERATURE AS AFFECTED BY DEPTH OF WATER TABLE

The success of the direct seeding where the water table was within 4 feet of the surface led to some further studies in 1939 on the role of soil temperature on these sites. Accordingly, in August 1939, records were made of soil surface temperatures at several stations with varying depths of water table.

TABLE 10. Measurements of jack pine seedlings on direct seeded field plots at end of second year after seeding.

	Soils with shallow water table (1 to 4 feet)		Soils with deeper water table (6 to 10 feet)	
	Average measurements	Basis, number of trees	Average measurements	Basis, number of trees
Height of tops (inches)	3.6	5	3.3	3
Depth of roots (inches)	10.6	5	13.0	4
Maximum spread of roots in furrows (inches)	24.1	3	21.8	4
Maximum spread of roots across furrows (inches)	20.7	3	17.4	4
Stem diameter (64ths inch)	7.4	5	5.5	6
Total oven-dry weight (grams)	2.02	5	1.13	6
Oven-dry weight of tops (grams)	1.48	5	.75	6
Oven-dry weight of roots (grams)	.74	5	.37	6
Top-root ratio (based on oven-dry weight)	2.00 :1	5	2.03 :1	6

Soil temperatures were obtained from thermometers laid in the bottom of the furrows in a field seeding area on an open sand plain which had a water table at depths ranging from 1.6 to 10 feet. The readings were taken on a moderately warm, cloudless day, and were taken only where plowing had been done to such a depth that all of the leached (A_2) soil horizon had been removed from the bottom of the furrow, thus exposing the light brown subsoil. It was felt that otherwise soil color differences might unduly influence the soil-surface temperatures.

The results are plotted in Figure 14 and the graphs indicate a considerable reduction in soil-surface tem-
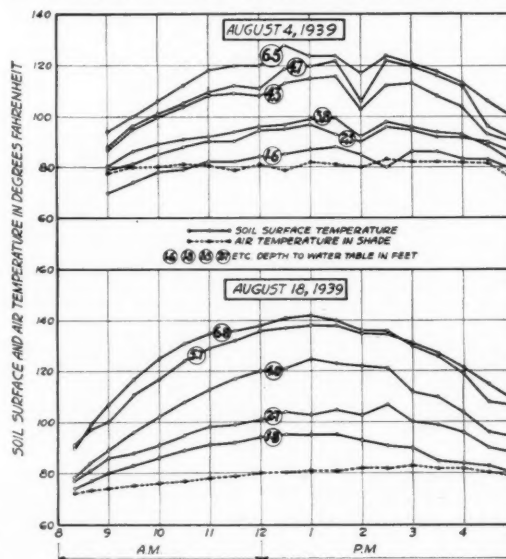

FIG. 14. Soil surface temperatures in relation to depth of water table in a fine sand soil, Nicolet National Forest, Wisconsin, 1939.

perature at the stations where the water table was within 4 feet of the surface, the extreme difference being 47 degrees observed on August 18, 1939. It is obvious that capillary rise of moisture from the water table was of decided benefit in decreasing soil-surface temperatures.

Although the air temperatures for the two days were almost identical, the surface cooling effect of a water table within 4 feet of the surface was more pronounced on August 18 than on August 4. This is attributed to the fact that the moisture content of the soil was somewhat different for the two sampling dates.[8]

The data for August 18 are particularly significant because they indicate that, where the water table was appreciably deeper than 4 feet, soil-surface temperatures of over 120° F. occur continuously for 6 hours. This is a most important fact because careful observations in forest nurseries and field seeding plots supplemented by thermograph records of soil-surface temperature indicate that with small conifer seedlings of jack, red, and white pines which are less than 30 days old, serious heat injury and actual death of the seedlings will occur on light sand or loamy sand soils, when the soil-surface temperature remains higher than 120° F. from 10 a.m. to 4 p.m.[9] The damage is increased if such temperatures occur day after day in late spring or early summer. It invariably shows up as a swelling or girdle, or in some cases as a lesion on the south or southwest side of the succulent stem of the tree just above the ground line. The seedling can recover from moderate heat injury, but if high soil temperatures prevail for a prolonged period, the seedlings eventually die. In nurseries soil-surface temperatures can be reduced by use of half shade provided by slat-wire snow-fence or by turning on the overhead sprinkling system. Under field conditions the few feasible methods of reducing heat injury to young seedlings on direct-seeded sites include taking advantage of planting sites with soils having fairly high water-retaining capacity which do not heat up like sands, or by selecting sandy open sites with a shallow water table. Measures to stimulate early and prompt germination of the seed by seeding in autumn, early spring sowing, or special pretreatment of seed are also feasible methods of reducing heat injury to seedlings. For the more critical conditions, seedling or transplant stock is required.

In order to rationalize the soil temperature information obtained in this study with the survivals indicated in Figure 13, the ratios of soil-surface temperature in the hottest part of the day to air tem-

[8] The moisture content of the top half inch to inch of soil is very important in determining how high surface temperatures become, because as soon as this layer of sand is fairly dry, the temperature will rise considerably, even though there is a fairly high soil moisture content below the thin layer of dry surface soil.

[9] The degree of injury or percentage of mortality caused by high soil-surface temperatures is dependent not only on intensity and duration of the high temperature, but also on the age of the seedling, amount of cortex present, and probably on soil color, composition of soil, and its ability to absorb, reflect, and conduct heat. Available moisture supply within rooting depth of the plants is also a factor having some bearing on injurious effect of high soil-surface temperatures.

perature in the shade for some of the data were plotted over depth of water table. These are presented in Figure 15, which shows that there is a fairly smooth trend in the ratio of soil-surface to air temperature, depending on depth to water table.
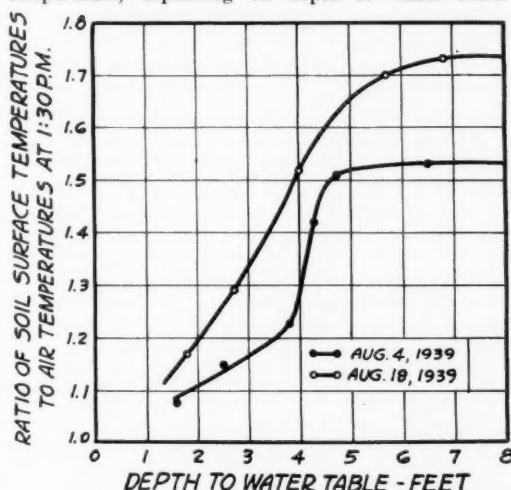

FIG. 15. Ratio of soil-surface temperature at 1.30 p.m. to air temperature in the shade in relation to depth of water table. Nicolet National Forest, Wisconsin. August 1939.

Since air temperatures of 85° to 95° F. are fairly common in June and July in this section of Wisconsin, it can readily be seen why the soil surface in open furrows in sand-plain areas often may attain temperatures of 130 to 150° F. or more and maintain them in this range for a considerable time. Figure 15 also gives a clue as to why losses attributable directly to heat injury are comparatively low for seeding sites where the water table is within 2.0 to 4.0 feet of the surface. It indicates that even under severe conditions soil temperatures are not likely to reach lethal limits for prolonged periods of time. Data obtained in August 1939 in this same area showed the following available soil moisture values for the top 6 inches of soil for several water-table depths: 1.8 feet, 10.3 percent; 2.7 feet, 7.4 percent; 4.6 feet, 2.3 percent; 6.8 feet, 1.4 percent. The data when plotted as available moisture over depth to water give a curve with the same trend as shown in Figure 13.

It is apparent from the temperature and soil-moisture data obtained that the subirrigated areas have two pronounced advantages over upland sand plains for direct seeding, namely, higher available soil moisture in the top 6 inches and lower soil-surface temperatures.

RESULTS IN A YEAR OF NORMAL PRECIPITATION

In the autumn of 1938 and spring of 1939 the direct seeding efforts were extended to another experimental plot on an open subirrigated sand plain, whose area was one acre and in which not only jack

pine but also red and white pine, black spruce (*Picea mariana* (Mill.) BSP.), white spruce (*Picea glauca* (Moench) Voss.), and European larch (*Larix decidua* Mill.) were used.

In the spring of 1939 the water table in this area lay at a depth of 1.0 to 3.1 feet below the surface. Water table fluctuations recorded at three points during the season showed that the water levels had lowered approximately 2.0 feet by late summer. In 1940 the water table showed a maximum fluctuation of 1.6 feet from early summer to autumn and maximum depth to water at any point in the plot was 5.5 feet.

In the seeding of the area a smaller amount of seed was used than in most of the previous tests. All seeding was with a hand-operated Planet Jr. garden seeder with the seed sown in a continuous even flow. Seeding was done in furrows 24 inches wide plowed in the summer of 1938.

The comparative results are given in Table 11. Observations showed that considerable germination took place within a month after sowing and was

TABLE 11. Results of direct seeding of conifers on subirrigated sand plains, Nicolet National Forest, Wisconsin.

Species	Date sown[1]	Pounds of seed sown per acre	Number of viable seeds sown per acre	Number of seedlings per acre		Tree percent[2]		Autumn 1940 stocking;[3] percentage of plots with—		
				Autumn 1939	Autumn 1940	Autumn 1939	Autumn 1940	1 or more seedlings per 10-foot plot	2 or more seedlings per 10-foot plot	3 or more seedlings per 10-foot plot
Jack pine	Autumn '38	0.33	28,944	1,815	944	6.3	3.3	75	43	13
Jack pine	Spring '39	0.11	9,648	1,125	545	8.6	5.7	43	20	3
Red pine	Autumn '38	0.60	25,220	1,125	763	4.5	3.0	53	35	8
Red pine	Spring '39	0.63	26,481	1,187	309	4.5	1.2	33	5	3
Mixed jack and red pines	Spring '39	0.29	18,813	3,303	1,544	17.5	8.2	68	43	28
White spruce	Autumn '38	0.33	7,600	73	0	1.0	0.0	0	0	0
White pine	Spring '39	0.65	2,132	109	18	5.1	0.8	3	0	0
Mixed black spruce & European larch	Spring '39	0.14	20,181	1,036	182	5.1	0.9	18	5	3

[1]Autumn sowing was done November 1, 1938; spring sowing on April 20, 1939. The total number of seed per pound for the various species used is as follows: jack pine, 119,200; red pine, 45,100; white pine, 24,300; white spruce, 200,800; black spruce, 347,900; European larch, 61,800.

[2]Tree percent represents percentage ratio of seedling stand obtained per acre to the total number of viable seeds sown per acre. Thus $\frac{1815}{28,994} \times 100 = 6.3$.

[3]One seedling in every 10-foot counting plot with the furrow spacing used in this experiment represents 726 seedlings per acre, two seedlings are equivalent to 1,452 per acre, and three are equivalent to 2,178 trees per acre. Counts are based on forty 10-foot counting plots in each species or mixture.

practically complete by June 14, except for the white pine and mixture of black spruce and European larch, for which some germination apparently occurred in midsummer. The table indicates that, of any individual species used, jack pine showed by far the highest tree percentage. This is attributed to the fact that this species germinates promptly within a week to two weeks if moisture conditions and depth of sowing are favorable; it makes rapid initial growth, has greater root penetration, and is more drought hardy.

Red pine was sufficiently successful to warrant considering its use in mixture with jack pine, provided a seeder is available that will handle seed of both sizes simultaneously without putting out more seed per unit of area than is desirable from a silvical and economic standpoint.[10] In fact, this is borne out by the mixed seeding of red and jack pines which showed a very satisfactory stand.

The white spruce and white pine did not show very good results and it is believed somewhat better results would have been obtained if stratified seed had been used. A considerable drop occurred in survival by the end of the second year and some of this loss is attributed to the smothering effect of leaves of low shrubs and other vegetation, such as sweetfern (*Myrica asplenifolia* L.), blueberry (*Vaccinum* sp.), bracken fern (*Pteris aquilina* L.), and quaking aspen, which collected in the furrow to a depth of one-half to one inch. The small seedlings were smothered in late fall and early spring by this mat of leaves and losses averaged 17 percent for jack pine, 20 percent for red pine, 33 percent for white pine, 50 percent for white spruce, and 77 percent for the mixture of black spruce and European larch. These losses were computed on the basis of seedlings present in the autumn.

Silvically, the use of jack and red pines on subirrigated sites might be questioned because they are ordinarily considered as species which prefer well-drained upland sandy moraines or outwash sands. Observations made in the national forests of Wisconsin and Michigan show considerable areas where these species are growing well on subirrigated sands (Figure 16).

In the periodic counts made during the first growing season, the chief cause of mortality was found to be heat injury on the parts of the plot where the water table was deeper than 4 feet, while on the other areas nipping of small seedlings by rodents and birds was the chief cause of mortality. The damage occurred chiefly while the seed coats were

[10] On a very favorable site, from 1,000 to 1,500 seedlings per acre, well distributed over the area, will result in a fairly successful stand, provided subsequent losses are not unduly high.

Conifer seed is expensive and must be used somewhat sparingly if direct seeding is to be considered of sufficient practical value to warrant its use instead of resorting to planting 1- to 4-year-old nursery stock. Average costs per pound of seed are: jack pine $5.90; red pine $7.16; white pine $1.74; white spruce $4.29; black spruce $10.95; European larch $3.04.

If one-fourth to one-half pound of seed is used per acre, total costs of direct seeding per acre (including ground preparation, seed, and labor, but not after-care such as overhead release) will be about $4.00 to $5.00 per acre. Planting costs using about 1,000 trees will range from $8.00 to $12.00 per acre.

still clinging to the cotyledons. Moderate dryness of the top 3 to 4 inches of soil was also a factor in loss where water table was deeper than 4 feet, even though soil moisture below the 4-inch level often was adequate. The loss due to soil dryness is accentuated because of the comparatively slow root development of most of the species used. Measurement of root systems of 5 to 10 trees of several species revealed the following average first-year depth of penetration: jack pine, 5.35 inches; red pine, 4.00 inches; white pine, 3.5 inches; white spruce, 1.75 inches. At the end of the second year they were 9.5, 5.4, 4.7, and 3.4 inches, respectively. These depths of rooting are in

Fig. 16. Fifty-year-old forest on sandy soil with permanent water table at 3 to 5 feet below the surface of the ground. Composition mainly red and white pines, with some black spruce, balsam fir, jack pine, and paper birch. Near Manistique, Michigan.

considerable contrast to those found in seedlings of the same age grown in fertile nursery soil where the rooting depth is usually two times as great as found on this field seeding area. It suggests that soil fertility may be a factor in extent of first-year root development. The average first-year length of top for the species listed above was 1.2, 0.9, 1.15, and 0.5 inches, respectively. At the end of the second year they were 2.8, 1.6, 1.8, and 0.8 inches.

BIOTIC FACTORS

In 1940 a small experiment was installed in an area adjoining the 1-acre plot sown in 1939 to study more intensively the reason for the rather low tree percent on direct seeded sites, which had very favorable moisture relations, but where counts of emerged seedlings did not account for anywhere near the total amount of viable seed sown. It was observed that rodents and birds, especially the former, dug up some of the seed in the 1939 seeding, but since the area was drill sown it was not entirely feasible to screen part of the area to exclude rodents and birds.

The spring of 1940 seeding consisted of 40 seed spots in each of four species of seed. No pretreatment was given seed except with white pine, which was soaked in concentrated commercial sulphuric acid for 10 minutes, then washed in running tap water for 5 minutes. Each spot contained 40 seeds. Half

of the spots were screened with a 4-mesh cone of hardware cloth 6 inches in diameter and 5 inches high. Half were left unscreened. Counts were made at frequent intervals during the season to follow progress of germination and to classify cause of loss. The area in which the seeding was done had a water table close enough to the surface to provide good moisture relations through the entire season, since the water table from May to October was never closer than within 1.5 feet of the surface nor deeper than 3 feet.

The progress of germination and survival in the four species is shown in Figure 17. The values are
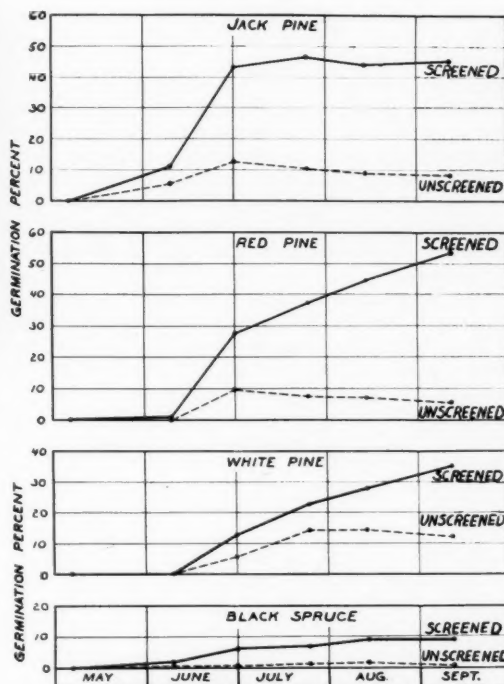

Fig. 17. Progress of germination in direct seeding of northern conifers on a ground-water podsol soil with half of seed spots protected from rodents and birds by screening. Seeded May 6, 1940. Nicolet National Forest, Wisconsin.

based on the relation of percentage of living seedlings to total number of viable seed sown, and the graph does not include seedlings which emerged from the soil and died.

An examination of the graph shows that there was a very significant difference in germination between the screened and unscreened spots with a maximum difference for red pine of 53.3 percent for screened and 5.4 percent for unscreened seed spots. This very great difference is attributed to pilfering of the seed from the unscreened spots by mice before germination occurred. Birds may have accounted for some of the loss, but frequent observations made in the

area lead to the belief that white-footed mice were largely responsible for the loss.

Red pine gave the highest germination in the screened spots, followed closely by jack pine; white pine was intermediate, and black spruce was a poor fourth. Losses attributed to mice are, therefore, 36.8, 48.0, 22.7, and 7.9 percent for jack, red and white pines, and black spruce, respectively.

Counts made at 5 different times throughout the season revealed that average postemergent losses for all four species were 3.3 percent for screened spots and 4.1 percent for unscreened spots. These losses were caused by postemergent damping-off, rodents, birds, insects, breakage by berry pickers, and smothering by leaves. The counts were probably not made frequently enough to identify all postemergent losses, but indicate that these losses for pine were small compared with those caused by mice. The seed unaccounted for ranged from 30.6 percent for screened red pine to 90.7 percent for unscreened black spruce. It averaged 49.7 percent for the three pine species. The failure of this percentage of the viable seed to emerge is attributed to preemergent damping-off, variable sowing depth, and perhaps to a lesser extent to insects which carried off the seed or had eaten it.

The germination values of 35 to 53 percent for screened spots for pine species are considered eminently satisfactory while the 9 percent obtained for black spruce is fair, considering the smallness of the seed and the delicacy of newly emerged seedlings.

The comparative stocking in seed spots is shown in Table 12. It will be noted that stocking was very good for the screened pine and fairly good for black spruce. If spots are considered which have 5 or more seedlings, the screened pine averaged 93 percent whereas the unscreened spots averaged 25 percent. The table also shows a striking contrast in the average number of seedlings in screened and unscreened spots, with the greatest difference in red pine where the averages were 19.2 and 1.9 seedlings per spot, respectively.

TABLE 12. Comparison of first-year stocking in direct seeding plots.

Species	Stocking in seed spots in the autumn of 1940								Average number of seedlings per seed spot [1]	
	Spots with 1 or more seedlings		Spots with 2 or more seedlings		Spots with 5 or more seedlings		Spots with 10 or more seedlings			
	Screened	Unscreened	Screened	Unscreened	Screened	Unscreened	Screened	Unscreened	Screened	Unscreened
	Per-cent	Per-cent	Per-cent	Per-cent	Per-cent	Per-cent	Per-cent	Per-cent	Per-cent	Per-cent
Jack pine...	100	55	100	55	90	25	70	10	14.5	2.7
Red pine...	100	55	100	35	95	15	80	5	19.2	1.9
White pine...	95	90	95	80	95	35	60	0	11.2	3.9
Black spruce.	85	25	55	5	10	0	0	0	2.1	0.2

[1] A total of 40 seeds was sown in each seed spot. There were 40 spots for each species, of which half were screened.

The conclusion drawn from the various direct seeding experiments is that biotic factors may rank in equal importance with available soil moisture, soil-surface temperature, and light in determining the success or failure of seeding. After the trees are several years old they are, of course, liable to injury by snowshoe hares and cottontail rabbits, and must run the risk of suppression by vegetation; but damage from these causes is negligible on open sites devoid of overhead cover which are preferred for direct seeding of conifers such as jack and red pines.

SUMMARY AND CONCLUSIONS

The most important single factor in success of forest planting and direct seeding in northern Wisconsin was found to be availability of soil moisture throughout the first growing season. Heavy losses occurred in dry years, while survivals were good in normal seasons. Available soil moisture was found to be adequate even in severe drought years on areas of shallow water table, but such conditions are found only on about 5 percent of the acreage of potential planting sites in the national forests of Wisconsin. Success on the remaining 95 percent of upland sites can be improved only by selection of more drought-hardy species, use of larger age classes, better methods of ground preparation, and taking maximum advantage of overhead cover.

Among the points of significance brought out in this study of ecological factors which affect success of reforestation in this part of the Lake States are the following:

1. Shallow water table had a marked effect on first-year survival of planted trees in drought years. Average survival of three different age classes in each of two species of trees, averaged 77 percent in areas where water table was from 3 to 6 feet from surface, and 28 percent on upland areas where water-table depth averaged 9 feet.

2. Available soil moisture in the ground-water podsol area was invariably from 3 to 4 percent higher than on typical well-drained upland jack pine sites. In the severe local drought year of 1937, available soil moisture for the rooting depth of the plants was below 2.5 percent for 64 consecutive days on the former site and only 31 days on the latter. Serious mortality occurred when available soil moisture for the 0- to 18-inch zone dropped below 2.5 percent for 40 consecutive days. In the lower part of the root zone of 12 to 18 inches it was below 2.5 percent for 49 days on the uplands and only 4 days on the ground-water podsols. In years of normal rainfall these values ranged mostly from 4 to 6 percent on uplands and from 6 to 10 percent on subirrigated areas.

3. Normality of rainfall is considered the single, most important factor in attaining successful results in the crucial first year. In a drought year when rainfall averaged 34 percent of normal for 5 consecutive months, May to September, inclusive, three different age classes of jack pine averaged 31 percent

in survival. The following year when rainfall was 104 percent normal these same age classes averaged 93 percent in survival.

4. In a year of severe drought, a light canopy of aspen 15 to 20 feet high and having a light intensity of 75 percent at breast height and 56 percent at 0.5 feet above ground made the difference between success and failure of 2-1 red pine. Under aspen cover survival was 69 percent and in the open only 16 percent. Losses directly attributed to drought were 9 and 46 percent, respectively, for the two sites.

5. The difference in survival in the open and under cover is attributed to marked reduction in evaporation rate. Evaporation losses under aspen were often only one tenth as high in midsummer as in the open. Evaporation rate is considered as having a strong influence on transpiration stress in plants, and under an overstory of aspen conifers receive considerable protection against excessive transpiration.

6. Studies of the root system of jack pine and red pine plantings one and two years of age showed that in the first year root growth was practically all downward to a depth of 10 to 22 inches, while in the second year strong lateral development occurred, with a maximum spread of 64 inches for jack pine and maximum depth of 23 inches. Jack pine was found to have about twice as great a second-year lateral root spread as red pine, and to this inherent characteristic of pronounced root extension is attributed the superior drought hardiness of jack pine.

7. Large age classes of stock invariably had somewhat better survival and larger root systems at the end of the first and second season in the field.

8. The most important causes of loss in recently established plantations were recognized as drought and May beetle larvae (*Phyllophaga* spp.). Other causes of loss are injury by snowshoe hares, nematodes, and poor planting. May beetle losses were much less in subirrigated sands than on uplands and actual losses for a 2-year period were 8 percent and 30 percent, respectively, for the two types of sites. Mortality after two years in the field was comparatively small.

9. Areas with permanent water table within 5 feet of the surface and not subject to excessive fluctuation were found to be excellent sites for direct seeding of jack pine. In the most extreme drought ever recorded in 28 years in the vicinity of Mountain, Wisconsin, the second-year stand in a direct seeding experiment was 6,300, 3,700, 1,400, 800, and 200 living trees per acre for areas with water table at 2, 3, 4, 5, and 12 feet, respectively. The seed was sown at the rate of one-fourth pound per acre by means of a garden seeder run in furrows prepared the previous season.

10. Other species which gave good initial survival in subsequent seeding experiments were red and white pines. Black spruce did fairly well but white spruce fared poorly.

11. The comparative ease of seedling establishment on subirrigated sandy sites was attributed to a constant and greater amount of available surface

moisture caused by the capillary rise of moisture from the water table. Available moisture in the surface 6 inches of the ground-water podsols was found to be from 5 to 10 percent, whereas on nearby upland sites it was as low as 1.4 to 2.6 percent in midsummer.

12. The presence of abundant surface-soil moisture had a profound influence on soil surface temperatures. In midsummer at 1 p.m. on a day when air temperature in the shade was 81° F., surface temperatures were found to be 95°, 103°, 125°, and 142° F. at stations where the water table was at 1.8, 2.7, 4.0, and 6.8 feet, respectively. Since recently germinated seedlings of the Lake States conifers often show injury or mortality from surface temperatures of 120° F., it was found that soil-surface temperatures would seldom reach the lethal range for a sufficient length of time to cause serious damage or death from heat injury in areas where ground water was within 4 feet of the surface.

13. The ratio of soil-surface temperature at 1 p.m. to air temperature in the shade was found to show a regular trend, depending on water table depth. Ratio of soil to air temperature was found to range from 1.5:1 to 1.75:1 on uplands while on sites with water table within 2 to 3 feet it ranged from 1.1:1 to 1.35:1.

14. One of the most important causes of failure of direct seeding was determined in a screening experiment as being due to rodents, probably white-footed mice. Germination percentages for screened seed spots of red pine were 53 percent at the end of the first year while unscreened spots showed only 5 percent survival.

15. Overwinter loss in furrow seeding caused by smothering of small seedlings by the fallen leaves of sweet fern and blueberry was the most serious factor in reducing stocking of 1-year-old seedlings.

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